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# LINKING PALEOBIOLOGICAL PATTERNS ACROSS GEOGRAPHIC SCALES: AN EXAMPLE USING UPPER MISSISSIPPIAN FOSSIL ASSEMBLAGES FROM THE ILLINOIS AND APPALACHIAN BASINS, USA

A Dissertation in

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by

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## ABSTRACT

A fundamental goal of evolutionary paleobiology is to understand how the composition, structure, and diversity of biotic assemblages have varied through space and time, in response to physical and/or biological perturbations. Historically, research on this topic has focused on reconstructing and understanding global biotic patterns throughout the Phanerozoic. This research program has greatly improved our understanding of the global history of marine biodiversity and helped to identify intervals of major biotic turnover throughout the Phanerozoic Eon. However, global level analyses mask important variability in the timing or magnitude of biotic change among regions or habitats and preclude an understanding of the processes that control faunal dynamics at regional and local levels. Work that integrates biotic patterns across spatial scales is needed to better understand the processes that combine to drive long-term ecological and evolutionary trends.

Here, I analyze regional patterns of marine taxonomic and ecologic diversity, turnover, and ecosystem structure across the onset the Late Paleozoic ice age (LPIA), using data that were collected within a highly resolved stratigraphic framework from the Illinois and Appalachian basins. In Chapter 2, I explore how global patterns of biotic turnover are expressed in the structure and stability of regional biotic gradients from the Illinois Basin during the LPIA - an interval noted for low global rates of faunal turnover. Gradient analyses reveal a marked shift in the structure of biotic gradients across the onset of the LPIA: in the pre-LPIA interval, depositional environments are clearly distinguished by ordination analyses and are dominated by distinct associations of taxa with modest habitat ranges. However, during the LPIA interval depositional environments are only weakly differentiated by ordination and are dominated by similar associations of taxa that had broad habitat ranges. Comparisons reveal that the structure of successive LPIA biotic gradients is nearly identical. Our results are consistent with findings from global level studies, which indicate that broadly adapted taxa (eurytopes) increased in importance following the start of the LPIA. However, unlike the global level, the regional increase in eurytopy was not linked to the extinction of narrowly adapted taxa in response to climate change. Instead, eurytopy increased as the geometry of the Illinois Basin shifted from a flat carbonate ramp, comprised of shallower water, higher stress environments in the pre-LPIA interval, to a steeper ramp comprised of deeper water, more stable habitats in the LPIA interval. Because eurytopic taxa tend to be extinction resistant and have lower rates of turnover their increased importance in late Paleozoic assemblages likely drove: (1) a previously documented pattern of decrease in regional-level turnover during the late Paleozoic and (2) a perceived pattern of greater persistence in late versus early Paleozoic biotic gradients.

In Chapter 3, I focus on regional taxonomic richness and compare regional diversity trends for the Illinois Basin to global patterns that have been reported previously in the literature. Sample standardized estimates of regional taxonomic diversity and guild diversity remain nearly constant across the onset of the LPIA, despite a documented 28% decline in global diversity. The transition to the LPIA is also associated with very low

levels of turnover: 76% to 92% of taxa persist from pre-LPIA sequences into the ice age interval. The onset of glacially driven high amplitude eustasy failed to affect significantly levels of regional diversity and faunal turnover during the LPIA interval. These results suggest that: (1) global and regional diversity patterns were decoupled across the onset of the LPIA and the timing or magnitude of extinction may have varied geographically across the globe; and (2) the major transition to the LPIA and associated high amplitude glacio-eustasy failed to strongly influence levels of regional diversity and turnover in the Illinois Basin. Thus, faunal persistence, not diversification or extinction, appears to be the normal biotic response to glacio-eustasy in the region, during the LPIA interval.

Chapter 4 provides the first study of its kind to compare geographic and temporal patterns of taxonomic richness, turnover, faunal composition, and ecosystem structure within and between correlative sequences in two separate depositional basins. This chapter builds upon the results displayed in chapters 2 and 3 by providing an important and comparable dataset from the Appalachian Basin, against which Illinois Basin faunal patterns can be compared. Therefore, this chapter makes a significant first step toward understanding the meaning of global LPIA biotic curves by resolving spatial complexity in faunal patterns between regions. Results from rarefaction and faunal turnover analyses indicate that taxonomic diversity, community structure, and faunal turnover did not vary significantly with geography, within or between depositional sequences. I suggest that interregional phenomena, including open connectivity between basins and the presence of similar environmental settings in each region, allowed for the establishment of comparable faunas in each basin; in turn these biotas responded in parallel ways to eustatic fluctuations between sequences. Following my discussion, I outline a research agenda for future regional studies that I believe will enrich the understanding of the biotic consequences of the LPIA and the meaning of LPIA global diversity data.

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# Chapter 1. Introduction

## Linking Biotic Patterns Among Spatial Scales

A central theme of evolutionary paleobiology is to understand the dynamics that govern the composition and diversity of fossil assemblages through space and time. Historically, much of the work in this area has focused on investigating diversity and turnover patterns at the global level, using large compilations of data that were mined from the published literature (e.g. Valentine 1969, Valentine and Moores 1970, Raup 1972, 1976a, 1976b, Sepkoski 1978, Valentine et al. 1978, e.g. Sepkoski 1979, Sepkoski 1981, Raup and Sepkoski 1982, Sepkoski 1984). These global level analyses helped to identify many of the central features of the fossil record, including major intervals of extinction, diversification, and faunal transition, and have formed the basis for much paleontologic research throughout the last 40 years.

Recently however, paleobiologists have become increasingly interested in understanding how synoptic global biotic patterns are manifest at the scale of local communities and regional ecosystems (see Miller 1997, Miller and Mao 1997, Jablonski 1998, Miller 1998, Patzkowsky 1999, Miller 2000, 2003, Novack-Gottshall and Miller 2003a, Patzkowsky and Holland 2003, Krug and Patzkowsky 2004, 2007, Patzkowsky and Holland 2007). Studies like these are beginning to inform on the degree to which global biotic patterns reflect processes emergent at local and regional geographic scales, as a direct result of the interactions of organisms to local and regional environmental disturbances. Results from this research suggest that global level patterns tend to mask variability in the timing or nature of biotic change between paleocontinents,

regions, or depositional environments and imply that a better understanding of the processes that combine to drive long-term ecological and evolutionary trends can be gained by integrating biotic patterns across spatial levels.

## Linking Taxonomic and Ecologic Patterns

Although taxonomic diversity, or richness, has commonly been used to document faunal patterns through space and time (e.g. Sanders 1968, Raup 1972, 1976a, Sepkoski 1978, Valentine et al. 1978, Sepkoski 1979, 1981, 1984, Alroy et al. 2001, Bush and Bambach 2004, Rohde and Muler 2005, Stanley 2007), it provides only one measure of the complexity of faunal assemblages. Thus, in addition to linking diversity patterns across geographic scales, it is necessary to examine multiple aspects of fossil assemblages to gain greater insight into the mechanisms that drive ecologic and evolutionary patterns in the fossil record (Rahel 1990, Wing 1993, McKinney 1998, Lupia et al. 1999, Pandolfi 2001, Novack-Gottshall and Miller 2003b, Bonelli et al. 2006, Kowalewski et al. 2006).

Abundance data offer one additional measure that can be used to characterize the complexity of fossil assemblages, and it has been shown to provide insight on ecological or evolutionary processes that cannot be gained from taxonomic data alone. For example, Bonelli et al. (2006) showed that the dominance (abundance) structures of recurring Middle Devonian coral-rich assemblages varied significantly across an interval of major physical disturbance, despite finding persistence in the species diversity and composition of these associations. These findings led the authors to refute previous

claims based upon taxonomic data, that these assemblages were exceptionally stable entities and were maintained by strong biotic interactions through geologic time (see Morris et al. 1995). Based upon their findings, Bonelli et al. (2006) argued that abundance data should play a stronger role in studies of the structure and stability of fossil assemblages because analyses of taxonomic data may mask important ecological attributes of fossil assemblages. Likewise, the analysis of ecological guilds provides another way in which paleoecologists can characterize the ecological complexity of fossil assemblages and measure paleoecological change associated with environmental or biological perturbations (Droser et al. 1997, Bottjer et al. 2001). Guilds represent groups of taxa with similar modes of life and feeding strategies (Root 1967, Bambach 1983, Dodd and Stanton 1990) and can be examined independently of taxonomic diversity or abundance data.

## Thesis Research

### Background

Here I analyze regional patterns of taxonomic and ecologic diversity, turnover, and ecosystem structure across the onset of the late Paleozoic ice age (LPIA), using data that were collected from Upper Mississippian (Chesterian Series) depositional sequences in the Illinois and Appalachian basins. The onset of the LPIA marked a major climatic transition from dominantly greenhouse conditions of the lower Mississippian to the cooler and more seasonal climates that characterized much of the Pennsylvanian and lower Permian (Crowell 1978, Caputo and Crowell 1985, Frakes et al. 1992, Crowell

1999). The ice age interval was dominated by high frequency (300-450 Kyr) and amplitude (~100 m) eustatic sea-level fluctuations that were driven by the repeated waxing and waning of glaciers on the southern continent of Gondwana (Wanless and Shepard 1936, Swann 1964, Veevers and Powell 1987, Walkden 1987, Dickens 1996, Smith et al. 2001b, Smith and Read 2001, Wright and Vanstone 2001, Al-Tawil and Read 2003, Al-Tawil et al. 2003, Isbell et al. 2003). These sea-level fluctuations are recorded as depositional sequences, or packages of rock bounded above and below by unconformities or their correlative conformities, that appear synchronously across Europe and North America during the late Mississippian (Butts 1922, Veevers and Powell 1987, Walkden 1987, Dickinson et al. 1994, Heckel 1994, Smith and Read 2000, Smith and Read 2001, Wright and Vanstone 2001, Raymond and Metz 2004). The surfaces bounding these depositional sequences can often be traced in the surface and subsurface across large geographic areas, within and between local basins, and are regarded as important stratigraphic surfaces that are useful for correlation (Pittman 1978, Dickinson et al. 1994, Brett 1995, 1998, Smith and Read 1999, 2000, Smith et al. 2001b, Smith and Read 2001, Nelson et al. 2002, Al-Tawil and Read 2003, Izart et al. 2003, Olszewski and Patzkowsky 2003). As such, the stratigraphic record of the LPIA is highly resolved.

The onset of the LPIA also coincided with significant biological changes in the marine realm. The start of the ice age was accompanied by a 28% decline of global marine diversity - a second order mass extinction - and was followed by an abrupt decline in rates of both origination and extinction (Stanley and Powell 2003, Stanley 2007). The long duration (approximately 50 Myr) of the weak biotic rebound that followed the LPIA biotic crisis sets it apart from the relatively quick recoveries following all other Paleozoic

mass extinctions (Hallam and Wignall 1997, Stanley and Powell 2003, Stanley 2007). In addition, the start of the LPIA altered the biogeographic structure of marine faunas by preferentially eliminating narrowly distributed tropical genera that were ill- equipped to cope with high frequency climate changes following the start of the ice age (Powell 2005, 2007); this caused the latitudinal gradient of biotic diversity to become distinctly more gentle during the LPIA relative to intervals before and after the ice age, due to the relative increase in genera with pandemic distributions (Powell 2005, 2007).

**Chapter 2**

In Chapter 2, I explore how global patterns of faunal turnover are expressed in the structure and stability of regional biotic gradients from the Illinois Basin (USA) during the late Paleozoic ice age (LPIA)- an interval noted for low global rates of taxonomic turnover. The results of this study are interpreted within the context of a globally recognized increase in the dominance of broadly distributed taxa (with characteristically lower rates of turnover), following the extinction of more narrowly distributed taxa (with higher rates of turnover) across the onset of the LPIA. Results indicate that the structure of biotic gradients shifted markedly after the start of the ice age, but then remained exceptionally stable through cycles of sea-level change during the LPIA interval. The change in gradient structure following the LPIA is associated with an increase in the dominance of taxa that were broadly adapted and widespread across all environments in the study area. Thus, there appear to be parallel increases in the importance of broadly adapted taxa at regional and global levels. Despite this, I suggest that regional biotic patterns were not driven by extinction, as has been reported at the global scale. Instead

the shifting geometry of the Illinois Basin played a dominant role in driving regional faunal patterns: relatively deeper-water, less stressed habitats formed as the Illinois Basin steepened during the LPIA interval. This deepening of the ramp acted to weaken differences between middle to outer ramp habitats, buffered taxa from environmental change, and produced a pattern of relative stability in biotic gradients throughout the LPIA study interval. Chapter 2 was written as a manuscript and submitted with my coauthor, M. E. Patzkowsky, to the journal *PALAIOS*. It was accepted for publication in May 2008.

**Chapter 3**

In chapter 3, I use taxonomic richness and guild richness data that were collected from the Illinois Basin to assess how regional and local levels of diversity and turnover varied between consecutive glacially driven depositional sequences and also across the onset of the LPIA. The results from this analysis are compared to those from published global level analyses and suggest that regional levels of taxonomic and guild richness persisted with little turnover throughout the study interval. These results indicate that regional and global patterns of diversity were decoupled following the start of the ice age and imply that the magnitude and timing of faunal change varied geographically. In addition, these results suggest that faunal persistence, not evolution or extinction, was the normal biotic response to the high-frequency eustatic changes that characterized the LPIA interval. This chapter was written as a manuscript and will be submitted shortly to one of three journals: *Paleobiology, PALAIOS, or Palaeogeography, Palaeoclimatology, Palaeoecology.* My advisor, M. E. Patzkowsky, will appear as a coauthor.

**Chapter 4**

In Chapter 4, I examine geographic variability in the responses of regional faunas to glacio-eustatic sea level changes during the LPIA interval. In this chapter, I use data that I collected from two consecutive depositional sequences that have been correlated over 300 km from the Illinois Basin into the Appalachian Basin. The taxonomic richness, and composition and structure of regional biotas are compared within each sequence across the two regions; patterns of turnover between depositional sequences are also compared. Results indicate that estimates of within-sequence taxonomic diversity did not vary between regions and that the composition and structure of biotic gradients were comparable in both basins. However levels of faunal turnover between sequences did vary minorly with geography, possibly due subtly regional differences in basin morphology between regions. I hypothesize that open connectivity between basins and the presence of similar environmental settings in each region, allowed for the establishment of comparable faunas within each region. In turn, these regional faunas responded in similar ways to eustatic changes associated with the LPIA, producing highly similar patterns of turnover in each basin. This study is the first of its kind to quantitatively compare regional marine biotas and their response to environmental change between depositional basins and provides evidence that regional phenomena may have played a large role in driving global biotic patterns during the LPIA interval, in contrast to the findings of previous global-level analysis of LPIA faunal patterns.

# Chapter 2. How are Global Patterns of Faunal Turnover Expressed at Regional Scales? Evidence from the Upper Mississippian (Chesterian Series), Illinois Basin, USA

## Introduction

Dissecting global scale patterns of faunal turnover into their local and regional components has emerged as an important focus of evolutionary paleoecology (e.g., Miller 1998, 2000). One reason for this has been the recognition that global patterns of biotic turnover are often manifested differently at the more local levels of depositional basins or paleocontinents; this has been true even when major intervals of global diversification or extinction have been studied, including the Ordovician radiation (Sepkoski 1988, Miller 1997, Miller and Mao 1997, Novack-Gottshall and Miller 2003a) and the Late Ordovician (Krug and Patzkowsky 2004, 2007) and end-Cretaceous (Jablonski 1998) extinction and recovery intervals. However, beyond the desire to understand similarities and differences in biodiversity patterns at global and local scales, how such times of global biotic change are manifested in the structure and stability of regional biotic gradients remains poorly understood.

The Chesterian Series (Upper Mississippian) of the Illinois Basin offers an ideal opportunity to examine how global biotic patterns of turnover are manifested at a regional scale. The Chesterian Series was deposited at the start of the late Paleozoic ice age (LPIA), which is an interval of time that was characterized globally by low rates of faunal turnover and was dominated by geographically widespread and long ranging, broadly-adapted taxa (Stanley and Powell 2003, Powell 2005, 2007). Within the Illinois Basin, Chesterian strata have been placed within a highly resolved environmental and

sequence stratigraphic framework of depositional sequences, which each represent one cycle of glacio-eustatic sea level rise and fall (Smith and Read 2000, Nelson et al. 2002). These sequences record the repeated re-establishment of a regional marine ecosystem to the study area (c.f. Olszewski and Patzkowsky 2001b) and can be used to measure the recurrence of biotic gradients during this interval of globally low faunal turnover and high-frequency environmental change.

In this paper we present gradient analyses for seven sampled fourth-order depositional sequences. These analyses are first used to describe the nature of biotic gradients throughout the 4 Myr study interval. We then use these associations to understand how documented decreases in global diversity and faunal turnover at the onset of the LPIA (Powell 2005, 2007), are manifested at the scale of the Illinois Basin and, further, how they are reflected in the structure and stability of regional biotic gradients.

## GEOLOGIC BACKGROUND

The Chesterian Series is well exposed at a number of roadcuts, quarries, and natural exposures across the Illinois Basin of Illinois, Indiana, and Kentucky. In this study, data were collected from 33 localities centered in southeastern Indiana and northwestern Kentucky (Fig. 2.1; Appendix C). The Illinois Basin was situated between 5˚ and 15˚ south of the equator during the Chesterian (Craig and Connor 1979, Scotese and McKerrow 1990), and was part of a widespread, shallow carbonate ramp that extended into western Canada (Craig and Connor 1979, Scotese and McKerrow 1990). The Chesterian Series records 11 high-frequency (~300-450 Kyr), unconformity

bounded, depositional sequences that have been correlated across the study area and which span the initiation of the LPIA (Fig. 2.2; Smith and Read 2000, Nelson et al. 2002).

**Pre-LPIA Interval**

Lower Chesterian strata (sequences 1-5) developed on a very gently sloping (< 5 cm/km), tidally influenced, carbonate ramp and were produced by moderate amplitude (10-30 m), glacio-eustatic sea level fluctuations prior to the onset of the LPIA (Fig. 2.2; Smith and Read 1999). It should be noted that, although present, siliciclastic facies make up only very small proportion of exposed pre-LPIA facies and are limited in abundance and distribution across the study area; for this reason we refer to the pre-LPIA interval as carbonate-dominated. Facies belts were controlled by local tidal energy rather than water depth; this produced a mosaic of habitats oriented in dip, rather than strike, parallel belts (Fig. 2.3; Smith and Read 1999).

The pre-LPIA interval contains four fossiliferous marine lithofacies: backshoal, intershoal, oolitic shoal, and skeletal bank (Fig. 2.3; see Carr 1973, Hunter 1993, Smith and Read 1999, Dodd et al. 2001, Nelson et al. 2002 for detailed discussions of depositional environments and stratigraphy of the Lower Chesterian interval). The backshoal facies is rare within the study area, as are all siliciclastic facies in the pre-LPIA interval (see above); when present it is dominantly fissile, olive green to dark grey fossiliferous shale that may be interbedded with wackestone and packstone. The backshoal habitat represents deposition in protected, shallow water, low energy settings behind oolitic shoals, during infrequent periods of siliciclastic influx (Smith and Read

1999). The intershoal consists of light grey to tan, massive, sparsely fossiliferous lime mudstones and wackestones that represent low energy muds deposited in-between and updip of oolitic shoals (Carr 1973, Hunter 1993, Smith and Read 1999). The oolitic shoal environment is represented by white to light gray, massive to cross and planar-bedded, skeletal, oolitic grainstones, which were deposited in high energy, shallow marine settings (Carr 1973, Smith and Read 1999, Smith et al. 2001b, Smith and Read 2001). The skeletal bank is dominated by light to dark gray, thick to medium and sometimes cross-bedded skeletal grainstones and packstones that were deposited in shallow water (< 10 m), medium to high-energy settings landward, in between, and seaward of oolitic shoals (Smith and Read 1999).

**LPIA Interval**

The Upper Chesterian interval (sequences 6-11) shows a marked shift toward mixed carbonate-siliciclastic dominated sequences that display significant subaerial exposure surfaces (Fig. 2.2; Smith and Read 1999, Smith et al. 2001b, Smith and Read 2001). In addition, these sequences were deposited on a more steeply dipping (< 7 cm/km), tidal and storm influenced ramp (see Fig. 2.4) and were produced by high amplitude (up to 95 m) glacio-eustatic sea level fluctuations associated with the waxing and waning of glaciers at the beginning of the LPIA (Smith and Read 2001). Unlike, the pre-LPIA interval, siliciclastic and deeper water facies are abundant and important components of all LPIA sequences. Facies belts are oriented strike parallel and change down dip in the Upper Chesterian interval due to the steeper slope of the ramp at that time (Smith et al. 2001b, Smith and Read 2001).

The LPIA interval contains 7 fossiliferous marine lithofacies: tidal flat, backshoal, intershoal, skeletal shoal, oolitic shoal, skeletal bank, and foreshoal (see Fig. 2.4; for detailed discussion of the depositional environments and sequence stratigraphy of the Upper Chesterian interval see Vincent 1975, Horowitz and Kelly 1987, Treworgy 1988, Harris 1992, Horowitz 1992, Smith and Read 2000, 2001, Nelson et al. 2002). The tidal flat facies consists of orange to grey, very fine-medium grained, cross to massive bedded, quartz sandstone that formed in a tide dominated, shallow marine environment (Huff 1993, Smith and Read 1999, 2001, Nelson et al. 2002). The grainstones and packstones of the skeletal bank facies lack the cross bedding and ooids seen in the pre-LPIA interval, but commonly contain graded beds. These differences likely reflect a more distal ramp position and suggest greater storm influence (Smith and Read 2001). Additionally, LPIA skeletal bank facies often contain a high proportion of quartz sand within their matrix. The foreshoal environment consists of medium to dark grey, thick to massive bedded, skeletal wackestones and mudstones that were deposited above storm wave base; the foreshoal represents the most distal environment sampled along the carbonate ramp (see Fig. 2.4).

## Faunal Data

### Data Collection

The dataset for this study is comprised of 12,874 individuals from 193 samples. Although effort was made to collect samples from all 11 depositional sequences in the study area, few samples were recovered from sequences 2-4 and 8 due to lack of

exposure of fossiliferous lithofacies; we therefore focus our study on the seven depositional sequences from which we could make more substantial collections (see Fig. 2.5).

At each sampling locality, care was taken to collect multiple (2-5), laterally distributed samples from exposed fossiliferous facies. This sampling strategy was used for two reasons: (1) it reduces the effects of spatial patchiness in fossil deposits and facilitates a more reliable estimate of the abundance characteristics of targeted fossil assemblages (Cobabe and Allmon 1994, Bennington and Rutherford 1999, Bennington 2003, Webber 2005) and (2) it allows for an assessment of variability in abundance at the outcrop scale (among lateral samples) – this provides a baseline against which larger scale variability can be assessed statistically (Hayek and Buzas 1997, Bennington and Rutherford 1999).

**Data Processing**

All samples were returned to the lab where they were cleaned with detergent, manually disaggregated, and examined using a binocular scope. All specimens were identified to the finest taxonomic level possible using the *Treatise on Invertebrate Paleontology* and taxonomic descriptions of Chesterian fossils contained in the literature (e.g., Weller 1916, Weller 1931, 1936, Sutton 1938b, McFarlan 1942, Moore 1948, Brookley 1955, Horowitz 1956, Rodriguez 1960, Perry and Horowitz 1963, Horowitz 1965, Thein and Nitecki 1974, Brezinski 1988, Chestnut and Ettensohn 1988, Busanus and Hoare 1991, Henry and Gordon 1992, Hoare 1993). Although many brachiopod, bivalve, gastropod, coral, and trilobite specimens were identifiable to the species level, a

large proportion could only be determined to the genus level. To maximize the use of as much data as possible, all of our statistical analyses were conducted at the genus level except for bryozoans, which were identified to family only. The minimum number of individuals (MNI) counting method (Gilinsky and Bennington 1994) was used to tally the abundances of fossil genera. This method adds the larger number of pedicle-brachial/left –right valves and unique fragments for bivalved organisms, or cephalon-pygidium counts for trilobites, to the number of articulated specimens within a sample and provides a conservative estimate of fossil abundances. Although there is no clear way to best measure the abundance of colonial organisms such as bryozoans and corals relative to that of bivalved taxa, we counted each 1 cm length of colony as one individual (see also Patzkowsky and Holland 1999, Holland and Patzkowsky 2004). This method at least allowed us to assess the relative importance of bryozoans and colonial corals in assemblages. These protocols yield average counts of 67 fossil individuals per sample (median = 50) and, in many cases, 200 or more individuals for single facies at each outcrop. A minimum sample size cutoff was not imposed in this study; however, samples were culled from the data set when preliminary multivariate analyses suggested that they were outliers and, in many cases, these were indeed samples with low total specimen counts.

## Quantitative Methods

Ecological gradients were analyzed using a variety of multivariate techniques including Q-mode and R-mode cluster analyses, detrended correspondence analysis

(DCA), nonmetric multidimensional scaling (NMS), and analysis of similarities (ANOSIM). In general, cluster analysis is an important tool that can aid in classifying data from large data sets into hierarchical groups based on a distance matrix (McCune and Grace, 2002). We used Q- and R-mode cluster analyses to identify biofacies, or groups of samples with similar taxonomic compositions and relative abundance structures (Ludvigsen et al. 1986). Although cluster analyses aided greatly in describing the biotic gradients by allowing us to characterize the faunal composition of specific portions of the gradient, we do not present cluster results for the sake of brevity. Results from cluster analyses are displayed in Appendix A.

Data were also subject to ordination by DCA (Hill and Gauch 1980) and NMS (Kruskal 1964). Ordination techniques are used to reduce and summarize the complex relationships among samples or species within a data set and to graphically array these along one or two axes that capture much of the primary variation in the data (Shi 1993, McCune and Grace 2002). We used ordination primarily to explore underlying environmental gradients in our dataset. Although results from DCA and NMS were similar, only DCA results are shown here because they tended to more successfully differentiate samples by depositional environment. Prior to ordination, sample counts were log transformed to emphasize the contributions of all taxa, rather than only the most abundant (McCune and Grace 2002). Counts were then subjected to a general relativization by row totals to account for differences in sample size that could potentially affect multivariate analyses (Shi 1993, McCune and Grace 2002). Removing the general relativization by row totals and then re-analyzing the log-transformed data matrix failed

to change the results or interpretations of this study. DCA was performed using DECORANA from the VEGAN package in R (R Project 2007).

We applied analysis of similarities (ANOSIM) to examine differences in the structure of biotic assemblages at a number of levels: (1) among depositional environments within a sequence; (2) among recurrences of a depositional environment through time; and (3) among sequences from the LPIA interval only. ANOSIM is a non-parametric technique that tests for the significance of differences among groups of samples, defined *a priori*, based upon the rank order of Bray-Curtis dissimilarity values (Clarke 1993). The strength of the ANOSIM test lies in its test statistic, *R*, which provides an absolute measure of compositional differences among the groups being evaluated, on a scale usually ranging from 0 (indicating that the ranks of similarities within and among groups are the same; i.e., the groups are indistinguishable) to 1 (indicating that the ranks of sample similarities within groups are more similar to each other than those between groups; i.e., the groups are different). It should also be noted that, in some cases, negative *R*-values can also be achieved (indicating that the ranks of sample similarities within groups are less similar than those between groups). Unlike the significance value (*p*), the *R*-value itself is not unduly affected by the number of replicates being compared among groups, and thus provides a relatively robust measure of biological dissimilarity even when sample sizes are small or vary among groups (Clarke and Gorley 2001). Generally, with $R > 0.75$, groups are distinct; with $R > 0.5$, groups are overlapping, but clearly different; with $R > 0.25$, groups overlap strongly; and with $R < 0.25$, groups are barely distinguishable (Clarke and Gorley 2001). ANOSIM was performed using ANOSIM from the VEGAN package in R (R Project 2007).

# Results

## Sequence 1

Ordination results indicate that carbonate dominated samples from the intershoal and skeletal bank environments overlap along low and intermediate axis 1 and 2 scores, but sort cleanly from samples from the siliciclastic muds of the backshoal habitat, which occupy positive axis 1 and 2 values (Fig. 2.6A). Given this sorting of samples, axes 1 and 2 appear to be partially correlated with substrate composition. The differentiation of carbonate and siliciclastic habitats in ordination space reflects differences in the composition and abundances of the taxa within these respective environment groups. For example, bryozoan and brachiopod-rich associations, consisting of fenestrate bryozoans and the brachiopods *Anthracospirifer, Ovatia,* and *Productus,* dominate the carbonate-rich environments of the intershoal and skeletal bank (see Appendix B). However, brachiopod and bivalve associations consisting of *Ovatia*, *Girtyella*, *Anthracospirifer*, *Martinia,* and the bivalve *Wilkingia,* comprise the siliciclastic rich backshoal habitat.

Taxa tend to sort along axis 1 following these habitat preferences (Fig. 2.7A). Taxa that occurred most commonly in the intershoal and skeletal bank lithofacies, including the bryozoans, the coral *Lithostrotian,* and the brachiopods *Productus, Dictyoclostus*, *Buxtonia, Orthotetes,* and *Cleiothyridina* tend toward low axis 1 scores (Fig. 2.7A). On the other hand, *Ovatia, Girtyella, Anthracospirifer, Wilkingia, Martinia* and other taxa with higher abundances in the backshoal tend toward high axis 1 scores (Fig. 2.7A). Other studies of Chesterian lithofacies and their associated fossil communities have also recognized a similar distribution of taxa among depositional

environments (see Gordon 1975, Gordon and Pojeta 1975, Fabian 1987, Butts 2005, 2007).

**Sequence 5**

As in sequence 1, ordination clearly segregates samples from carbonate and siliciclastic habitats along DCA axis 1 (Fig. 2.6B). Samples from the oolitic shoal habitat, a carbonate environment, occupy low and intermediate axis 1 values, while samples from the siliciclastic-rich sediments of the backshoal environment occur at the most positive values. In addition to reflecting a gradient of substrate composition (from carbonate to siliciclastic), axis 1 may also reflect a water energy gradient (from higher to lower energy) or a substrate consistency gradient (from firm to soft substrates).

Taxa sort along axis 1 following a similar, but not identical, distribution to that shown in sequence 1 (Fig. 2.7B). For example, fenestrate bryozoan taxa again tend toward low and intermediate axis 1 scores and occur in higher abundances in a carbonate-rich environment (the oolitic shoal), rather than in the siliciclastic-rich backshoal habitat (see Appendix B). *Wilkingia* also follows preferences it showed in sequence 1; it attains its greatest abundance in the backshoal environment (see Appendix B) and again occupies a positive axis 1 score. The productid brachiopods, *Ovatia* and *Productus,* plot at low axis 1 scores, and occur in the oolitic shoal environment in sequence 5. The oolitic shoal habitat was subject to higher water energy conditions and contained firmer substrates than the environments in which these taxa occurred in sequence 1. Although it is tempting to conclude that these taxa have switched their habitat tolerances in sequence 5, other studies have noted that these spiny productid genera have broad environmental

tolerances and can inhabit firm and soft substrates and low and high energy settings (Fabian 1987, Butts 2005, 2007). Like sequence 1, *Anthracospirifer* was present in both carbonate and siliciclastic habitats and retained its positive score along axis 1. Similarly to *Productus* and *Ovatia*, *Anthracospirifer* is another brachiopod genus that is known to occupy and tolerate a range of habitat types and environmental conditions (Gordon 1975, Fabian 1987).

**Sequence 6**

DCA indicates a modest overlap of depositional environments in sequence 6 (Fig. 2.6C). For example, oolitic shoal samples occupy low scores on axis 1 and overlap with a few intershoal samples, which tend to occupy low to intermediate axis 1 values. Samples from the backshoal habitat occupy intermediate axis 1 and low axis 2 scores and separate cleanly from the other environments. This is also true of samples from the skeletal bank facies, which tend to have the highest axis 1 values. Given this sorting of environments, axis 1 appears to reflect a nearshore to offshore gradient: inner ramp facies occupy low to intermediate scores and middle ramp facies tend to high axis 1 scores. Unlike the ordinations for sequences 1 and 5, no major distinction is made between carbonate and siliciclastic habitats in sequence 6.

Fenestrate bryozoans, which have been shown to be adapted to a variety of environments and substrates (Perry and Horowitz 1963, McKinney 1972, McKinney and Gault 1980), were widespread across the ramp and important components in all four of the inner to mid ramp habitats in sequence 6 (see Appendix B). In addition to these taxa, *Pentremites* blastoids, trepostome bryozoans, and the brachiopods *Composita*, *Dielasma*,

and *Reticulariina* were also present in the skeletal bank facies and tended to occupy high axis 1 scores (Fig. 2.7C). Other studies have found that similar faunal associations occur within pack and grainstones facies that are inferred to represent a comparable inner to mid-ramp setting (see Fabian 1987, Butts 2005). *Orthotetes, Anthracospirifer*, *Ovatia, Productus,* and *Martinia* tend toward negative axis 1 scores and are common in the lower energy and softer substrate settings of the backshoal and intershoal habitats in sequence 6 (see Appendix B). Like sequence 5, *Ovatia* and *Productus* also inhabited the oolitic shoal environment; their presence provides further support for the hypothesis that spines may provide anchorage in higher-energy settings, in addition to support on soft soupy substrates (Leighton 2000).

**Sequence 7**

Depositional environments are more poorly differentiated in sequence 7 than they are in the ordinations of sequences 1, 5, and 6 (Fig. 2.6D). For example, samples from the backshoal and skeletal bank environments overlap markedly on the left of axis 1, suggesting only weak faunal differences between these habitats. Indeed, fenestrate bryozoans and *Reticulariina* completely dominate these environments, where they comprise 46% to 66% of the total individuals sampled (see Appendix B). Weaker differentiation exists between skeletal bank and foreshoal samples along axis 1, as these intermingle at intermediate axis 1 values. Despite the weaker habitat differentiation displayed in the ordination of sequence 7, DCA axis 1 approximates a nearshore to offshore gradient much like sequence 6: inner and middle ramp habitats occupy low to

intermediate values and samples from the outer ramp (foreshoal) tend toward positive values.

The distribution of taxa among habitats and along DCA axis 1 is similar to that shown for sequence 6 (Fig. 2.7D). For example, fenestrate and other bryozoan taxa are common within the inner and middle ramp and are especially abundant in the skeletal bank habitat (Appendix B). In sequence 7, fenestrates plot at intermediate axis 1 values. Similarly to sequence 6, *Pentremites* blastoids, *Reticulariina*, and *Eumetria* are most common along the inner to middle ramp (in the backshoal and skeletal bank habitats). These taxa occupy negative axis 1 scores in sequence 7. *Productus*, *Ovatia*, *Dictyoclostus*, *Echinoconchus*, *Orthotetes*, and *Martinia* tend to positive axis 1 scores and again inhabit a low energy, soft substrate environment – in this particular case, the foreshoal habitat.

**Sequence 9**

Similarly to sequences 6 and 7, ordination analyses suggest that samples sort along a nearshore to offshore gradient in sequence 9: samples from the skeletal bank habitat occupy low DCA axis 1 scores, while samples from the foreshoal environment tend toward high axis 1 values (Fig. 2.6E). Differentiation of skeletal bank samples along axis 2 appears to be driven primarily by differences in the abundance of fenestrate, rhabdomesid, and trepostome bryozoan taxa, as well as the brachiopod genus *Martinia*. For example, these four taxa account for over 50% of the individuals recovered from the skeletal bank samples that occupy negative axis 2 values. In contrast, these taxa comprise only 6.3% of the individuals collected from the skeletal bank samples that

occupy positive axis 2 values. These samples are instead dominated by an assortment of spiriferid and productid brachiopod genera. These faunal differences likely reflect subtle environmental heterogeneity within the skeletal bank facies, as sand-poor skeletal bank samples occupy low axis 2 scores and sand-rich samples occur at high axis 1 scores.

The distribution of taxa among habitats and along axis 1 is similar to that shown in earlier sequences (Fig. 2.7E). For example bryozoan taxa, *Pentremites* blastoids, *Reticulariina,* and *Eumetria* again tend toward the middle ramp (skeletal bank) and occupy low and intermediate axis 1 scores, while *Productus* and *Ovatia* again tend to the outer ramp (foreshoal) and occupy high axis 1 scores. Along axis two, *Chonetes, Spirifer, Cleiothyridina, Orthotetes, Reticulariina,* and *Pentremites* tend toward sandier skeletal bank samples, while the bryozoans, *Martinia, Girtyella,* and the bivalve *Nuculopsis* tend toward relatively more muddy skeletal bank samples.

**Sequence 10**

There is marked overlap among depositional environments in sequence 10 (Fig. 2.6F). Fenestrate bryozoan and brachiopod-rich samples from the inner and middle ramp (tidal flat, backshoal, skeletal shoal, and skeletal bank habitats) clearly overlie one another, but again are mostly separate from the foreshoal samples. In order to more fairly compare the ordination of sequence 10 with the ordinations from all other sequences we removed tidal flat samples from the analysis; this habitat was not sampled in any other sequence. Despite this, the distribution of environments along DCA axis 1 was unchanged and, like sequences 6, 7, and 9, reflects position on the ramp: inner and middle ramp environments tend to negative and intermediate values along axis 1 while

outer ramp habitats tend to positive values. Axis two reflects a gradient from sand-rich substrates at positive scores to mud-rich substrates at negative scores.

Taxa appear to sort in a similar way to that shown for sequences 6, 7, and 9 (Fig. 2.7F). The inner to middle ramp environments tend toward being bryozoan dominated (see Appendix B), but are comprised of a diverse suite of taxa including *Pentremites, Eumetria, Cleiothyridina, Reticulariina, Composita,* and *Punctospirifer.* On the other hand, *Productus, Anthracospirifer, Martinia, Girtyella,* and *Spirifer* tend toward the low energy, soft substrate setting of the outer ramp (foreshoal). Similarly to sequence 9, *Torynifer, Eumetria, Cleiothyridina,* and *Reticulariina* tend toward sandier substrates while, *Productus, Anthracospirifer, Martinia, Girtyella,* and *Spirifer* tend toward muddy substrates.

**Sequence 11**

Like previous LPIA sequences, depositional environments are weakly discriminated by ordination analysis (Fig. 2.6G): backshoal samples tend toward low and intermediate scores, skeletal shoal samples toward intermediate values, and skeletal bank samples tend toward intermediate and high values. The sorting of environments along axis 1 again appears to reflect position on the ramp, with nearshore environments occupying slightly negative and intermediate values and middle ramp environments occurring at intermediate to positive values.

As was true in earlier sequences, inner and middle ramp environments tended to be heavily dominated by bryozoan taxa (see Appendix B); this is especially true of the fenestrates, which alone comprised over 53% of the individuals collected from the

skeletal bank and backshoal facies. Other taxa, including trepostome and rhabdomesid bryozoans and an assortment of spiriferid brachiopods (*Reticulariina*, *Anthracospirifer*, *Composita*, *Cleiothyridina*) are also important components of these environments and occupy intermediate and positive axis 1 scores (Fig. 2.7G). Like earlier sequences, *Productus* and *Ovatia* again inhabit a low energy, soft substrate environment - in this particular case, the backshoal environment of the inner ramp. These taxa occupy negative axis 1 scores.

## Discussion

### Pre-LPIA Gradient Ecology (Sequences 1 & 5)

The structures of the biotic gradients in pre-LPIA sequences (1 and 5) are similar, despite uneven sampling of environments between sequences. For example, ordinations for sequences 1 and 5 display a differentiation of carbonate and siliciclastic environments along DCA axis 1 and suggest that substrate composition was a primary control on the distribution of taxa. Taxa tend to occupy similar, although not identical, positions along axis 1 relative to the distribution of carbonate and siliciclastic habitats: *Productus*, *Orthotetes*, and fenestrate bryozoans are common in carbonate-rich environments, while the bivalve *Wilkingia* occurs in siliciclastic-rich habitats. Other taxa, such as *Anthracospirifer* occur in moderate to high abundances in both carbonate and siliciclastic facies. Figure 2.8 and table 2.2 illustrate further the distribution of taxa among environments during the pre-LPIA. These data suggest that while there is substantial compositional similarity among environments (Fig. 2.8), each can be distinguished based

upon abundances of their respective dominant taxa (Table 2.2). DCA ordinations of samples coded by environment (see Fig. 2.6A-B) also display little overlap among environments. ANOSIM tests for faunal differentiation among environments for sequence 1 and 5 support the ordination results and indicate that environments are very distinct from one another ($R$ = 0.819 and 0.885 respectively for sequences 1 and 5; see Table 2.3).

Caveats

At least some of the differences we observed among depositional environments in the pre-LPIA interval could be driven by small sample sizes; this is especially likely for the comparisons involving the oolitic shoal or skeletal bank facies because they are represented by only a few samples. We would undoubtedly have witnessed more faunal overlap among environments in the pre-LPIA interval had we been able to collect more samples from each habitat.

To the best of our knowledge, there have been no recent quantitative paleoecological studies focused on the Ste. Genevieve and Paoli intervals (sequences 1-5) from which we could supplement our data to account for the sample bias described above. However, presence-absence datasets from Weller (1916) and Batchelor (1948) at least provide data points against which we can compare the completeness of our taxonomic lists for these intervals. These two studies suggest that, on the whole, our sample of brachiopod, bryozoan, and trilobite taxa from sequences 1 and 5 are mostly complete, save a single brachiopod genus - *Pugnoides*. That said, our list of bivalve and gastropod taxa for these sequences is far less complete, although the bivalves and

gastropods recovered from our samples were often very poorly preserved and could not be identified to a taxonomic level below "bivalve or gastropod indet." Because Weller's (1916) study specified that data was included from the oolitic shoal environment, we were able to directly compare our data to his for this environment. This comparison suggests we are missing only a single occurrence – the brachiopod *Orthotetes*- from the oolitic shoal environment, despite limited sampling. Although Weller (1916) and Batchelor's (1948) studies do not report abundance data, we find it reassuring that even with the small total number of samples we collected, we appear to have captured a representative faunal list for sequences 1 and 5 as a whole, and for at least one of the two poorly sampled environments in this interval. Thus, although we cannot discount the importance of the role that small sample sizes might have played in producing faunal differences among pre-LPIA environments, results from our literature-based comparisons suggest that the faunal differentiation is likely real and biologically meaningful.

**LPIA Gradient Ecology (Sequences 6-11)**

There is a change in the structure of biotic gradients in the LPIA interval: depositional environments are more poorly differentiated in ordination space and sort along a nearshore offshore gradient, rather than one driven by substrate composition. The distribution of abundant taxa among habitats and along DCA axis 1 is highly conserved through time: bryozoan taxa, *Pentremites*, *Eumetria*, and *Reticulariina* tend toward inner and middle ramp habitats, while *Productus, Ovatia, Orthotetes,* and *Martinia* tend toward the soft substrate, low energy environments of the foreshoal (or intershoal when present). Taxa appear to be even more broadly distributed among

environments in the LPIA interval (Fig. 2.9) and, in almost every case, habitats are characterized by a consistent list of common and rare taxa through time. Fenestrate bryozoans are particularly important components of LPIA habitats and are dominant in many of the environmental zones along the ramp (see Fig. 2.9 and Table 2.4). The results of ANOSIM tests for differentiation among habitats within each sequence indicate substantial overlap of faunas from different environments during the LPIA, as shown by the small *R*-values associated with each sequence (Table 2.3A, B). The lack of within sequence habitat differentiation is likely due to the substantial number of shared taxa among habitats and dominance of fenestrate bryozoans in almost all facies as described above. We note that even when we removed bryozoan taxa, which might have been expected to show broader habitat tolerances because they were less well resolved taxonomically (i.e., they were identified only to the family level, but all other taxa were identified to genus) the outcomes of ANOSIM tests are nearly unchanged (see Table 2.3C, D). Interestingly, results from sequence 6 indicate that its habitats are only slightly more similar to one another than observed for the pre-LPIA interval. This suggests that the assemblages within sequence 6 are somewhat transitional between the well-differentiated pre-LPIA assemblages and weakly differentiated LPIA assemblages.

Caveats

Due to sampling differences between the pre-LPIA and LPIA intervals, these gradient differences need to be interpreted with some caution. Pre-LPIA sequences contain fewer: (1) total environments and (2) total samples than LPIA sequences (see Fig. 2.5, Table 2.3). This raises the possibility that increased sample sizes may be driving the

trend toward lower ANOSIM *R*-values in the LPIA interval. Indeed, there is a moderate, although insignificant, correlation between ANOSIM *R*-value and the number of samples ($r = 0.72$; $r^2 = 0.53$; $p = 0.06$).

In an attempt to account for any potential sampling biases, a second set of ANOSIM tests were performed. In these analyses, we attempted to standardize the pre-LPIA and LPIA intervals by environment, since fewer environments are sampled during the pre-LPIA; in other words, environments that were sampled in the LPIA interval, but not in the pre-LPIA interval (e.g., tidal, skeletal shoal, foreshoal) were removed from the analysis (Table 3B). This treatment of the data effectively reduced the total number of samples collected for each LPIA sequence (with the exception of sequence 6) and enabled a more fair comparison because faunal differentiation for each sequence was examined only among a set of consistently recurring habitats. Despite this treatment, ANOSIM *R*-values still show a marked decrease in the LPIA interval; importantly, this trend is not strongly correlated with the number of samples ($r = 0.22$; $r^2 = 0.05$; $p = 0.67$). This suggests that, at least among habitats that recurred consistently through the study interval, faunal differentiation decreased among habitats during the LPIA interval in the Illinois Basin.

**Linking Biotic Patterns at the Global and Regional Scales**

Previous analyses of the biotic response to the onset of massive glaciation in the late Mississippian indicate that latitudinal diversity gradients weakened markedly (Powell 2005, 2007). This change has been attributed to the preferential elimination of geographically restricted, stenotopic genera that may not have been adapted to high

frequency climate or sea level changes associated with the LPIA (Powell 2005, 2007). The loss of these narrowly adapted forms left the oceans dominated by taxa with wide latitudinal ranges that would tend to have broader habitat preferences and be more resistant to extinction in the face of varying environmental conditions (Stanley 1979, 1990, 2007).

The results of our regional study are consistent with some of the observations made at the global and latitudinal scales for the LPIA interval: regional biotic gradients were less strongly structured in the tropical Illinois Basin and very little faunal differentiation existed among depositional environments; in other words broadly adapted, or eurytopic taxa, appear ubiquitous across the ramp in the Illinois Basin during the LPIA interval (Fig. 2.9). However, the results from Chapter 3 indicate that, unlike the trajectory of global diversity, regional generic diversity in the Illinois Basin failed to decrease at the onset of the LPIA. This begs the question: in the absence of a regional extinction of stenotopic taxa, why are local communities less differentiated among habitats in the LPIA sequences?

One potential cause for changes in the regional structure of assemblages following the start of the LPIA is that the geometry of the Illinois basin changed from that of a carbonate platform in the pre-LPIA interval, to a shallow carbonate ramp in the LPIA interval (see Smith and Read, 1999, 2001). In the pre-LPIA interval, sequences record shallower water environments that were deposited in less than 10 m water depth (Smith and Read, 1999). Given their shallow depth, these environments were likely higher stress settings and subject to frequent fluctuations in environmental conditions. Shallow water, high stress environments tend to be characterized by distinctive faunal

associations that are dominated by more opportunistic taxa with restricted habitat ranges (Bambach 1977, Kowalewski et al. 2002, Scarponi and Kowalewski 2007). The LPIA interval, on the other hand, is characterized by deeper water environments (see Smith and Read 2001) that would tend to have more stable environmental conditions and host communities that are less well-defined (Brett 1998). The results of our study are consistent with these expectations: faunal differentiation is strongest among the relatively shallower water habitats of the pre-LPIA interval, and weaker among the deeper water habitats that typify the LPIA interval. Thus, although the extinction of stenotopes played a major role in producing global level biotic patterns during the transition to the LPIA (Stanley and Powell, 2003; Powell, 2005, 2007), it does not appear to have played a strong role in driving regional biotic patterns in the Illinois Basin – despite coincident increases in eurytopy at both the global and regional levels. Instead, regional ecological changes in the Illinois Basin coincide closely with regional changes to basin geometry. Therefore, distinct processes appear to have driven very similar ecological changes at the global and regional levels during the transition to the LPIA.

**Comparison to Other Studies of Regional Biotic Turnover During the late Paleozoic**

Detailed quantitative studies of recurring Paleozoic biofacies and biotic gradients have reported varying levels of faunal persistence across a multitude of spatial and temporal scales. For example, in their study of brachiopod dominated biofacies from the Upper Ordovician of the Cincinnati Arch region, Holland and Patzkowsky (2004) found that ecosystems were dynamic during a period of oceanographic and biotic change prior to the late Ordovician glaciation; ecosystem changes included the absence of particular

biofacies in some sequences despite suitable facies, variability in the composition and dominance structure of biofacies, and departures in the preferred environmental tolerances of individual species. On the other hand, in a quantitative study of recurrence in Middle Devonian biofacies, Brett et al. (2007) reported persistent biofacies and biotic gradients, through a 5-6 Myr interval in the Appalachian Basin. They presented evidence for strong similarities in species richness, composition, guild structure, and species environmental tolerances, but not necessarily in species ranks or abundances (see also Bonelli et al. 2006), despite evidence for biotic and environmental perturbation.

Here, in addition to documenting similar faunal gradients throughout the LPIA interval, we also observe high levels of faunal persistence. The results from ANOSIM tests for faunal differences among LPIA sequences and also for differences among assemblages within recurring environments yield low *R*-values, which indicate a very high level of faunal persistence: faunal assemblages from LPIA sequences are barely distinguishable ($R$=0.179). Moreover, comparisons of the faunas from recurring environments show a similar pattern; assemblages from the backshoal, skeletal bank, and foreshoal all persist in their respective environments relatively unchanged through the LPIA study interval ($R$=0.178, $R$=0.275, $R$=–0.137, respectively), regardless of whether or not we include poorly identified bryozoan taxa in the analysis. We attribute this high degree of temporal persistence to the presence of a similar suite of broadly adapted taxa within each sequence (see Fig. 2.8), which were capable of persisting through high-frequency climate and eustatic changes associated with the LPIA.

The pattern described above is broadly consistent with results from other studies that have quantified biofacies or gradient recurrence during later phases of the LPIA,

including Upper Pennsylvanian crinoid biofacies (Holterhoff 1996), Pennsylvanian and Permian brachiopod and bivalve biofacies (Olszewski and Patzkowsky 2001b), and Pennsylvanian soft-bottom marine invertebrate assemblages (Bennington and Bambach 1996). Each of these late Paleozoic studies reports at least broad recurrence of biofacies or community types, rather than finding evidence for marked changes in the habitat tolerances of species and/or major changes to the composition of individual biofacies. This raises an intriguing question: why do patterns of biofacies stability tend to differ between the early and late Paleozoic (c.f. Patzkowsky 1999)? Perhaps, as shown here, late Paleozoic (Carboniferous-Lower Permian) biofacies tend to appear more persistent than those of the Upper Ordovician due to the increase of more eurytopic forms; a number of studies on different fossil organisms have demonstrated that because eurytopic taxa are less affected by fluctuating environmental conditions they are more resistant to extinction, have greater taxonomic durations, and characteristically lower rates of turnover (Hansen 1978, 1980, Buzas and Culver 1984, Jablonski 1986, Stanley 1986, Vrba 1987, Norris 1991, 1992, Baumiller 1993, Gili and Martinell 1994, Kammer et al. 1997, McKinney 1997, Kammer et al. 1998). A full test of this idea is outside of the scope of this paper and requires more data from detailed regional studies of biofacies and biotic gradients from the early and late Paleozoic. However, this hypothesis is consistent with, and provides one possible explanation for, the observation that the magnitude and frequency of regional turnover episodes was low during the late Paleozoic (Olszewski and Patzkowsky 2001a), despite abundant evidence for high-frequency climate and eustatic changes that characterize much of this interval. In addition our results are also consistent with, and appear to be a regional manifestation of, a well-documented global

decrease in late Paleozoic rates of origination and extinction (Raup and Sepkoski 1982, Flessa and Jablonski 1985, Gilinsky 1994, Sepkoski 1998, Stanley 2007), which suggests that late Paleozoic regional ecosystems were characterized by eurytopic taxa that resisted extinction even in the face of high frequency environmental perturbations.

## Conlcusions

The major findings of this study can be summarized as follows:

1. Sequences in the pre-LPIA study interval are characterized by a similar gradient structure. Depositional environments are clearly differentiated within ordination space along an inferred gradient of carbonate to siliciclastic substrates. Taxa sort along this gradient consistently in sequences 1 and 5, with bryozoan and brachiopod-rich assemblages tending toward carbonate environments and brachiopod and bivalve-rich assemblages tending toward siliciclastic habitats.
2. Sequences in the LPIA study interval display a different ecological structure from that observed in the pre-LPIA interval. Depositional environments are weakly differentiated within ordination space along an inferred nearshore-offshore gradient. Taxa sort along this gradient consistently in sequences 6-11, with fenestrate bryozoan-dominated assemblages occupying nearshore environments and productid brachiopod-rich assemblages characterizing the offshore.
3. Weaker faunal differentiation is observed among environments in the LPIA interval: most environments are dominated by the same small set of taxa that appear in similar rank abundances. The weaker faunal differentiation in the Illinois Basin parallels a

biotic shift occurring at the global scale, where it has been recognized that genera with large geographic ranges and, perhaps, broad habitat preferences came to dominate during the LPIA following the extinction of stenotopic forms not capable of persisting under variable climates (Powell 2005, 2007). However, climate-related extinction played no role in reducing faunal differentiation among communities at the regional scale of the Illinois Basin. Instead, taxa became more widely distributed among LPIA habitats as the geometry of the Illinois Basin changed from a shallow carbonate platform in the pre-LPIA interval, to a relatively deeper water ramp during the LPIA.

4. Faunal assemblages persist with high fidelity in recurring depositional environments, despite evidence for high-frequency environmental fluctuations during the LPIA interval. We suggest that this pattern reflects the dominance of broadly adapted, eurytopic taxa that were resistant to high-frequency environmental changes during this early portion of the ice age. We suggest that the domination of eurytopic forms shown here and in previous global level studies of late Paleozoic biotas (Powell 2005, 2007) provides a potential explanation for: (1) an observed decrease in the frequency and magnitude of regional turnover events during the late Paleozoic (Olszewski and Patzkowsky 2001a); and (2) perceived differences in patterns of biofacies stability throughout the Paleozoic, with less persistent assemblages dominating the early Paleozoic and more persistent assemblages characterizing the late Paleozoic.

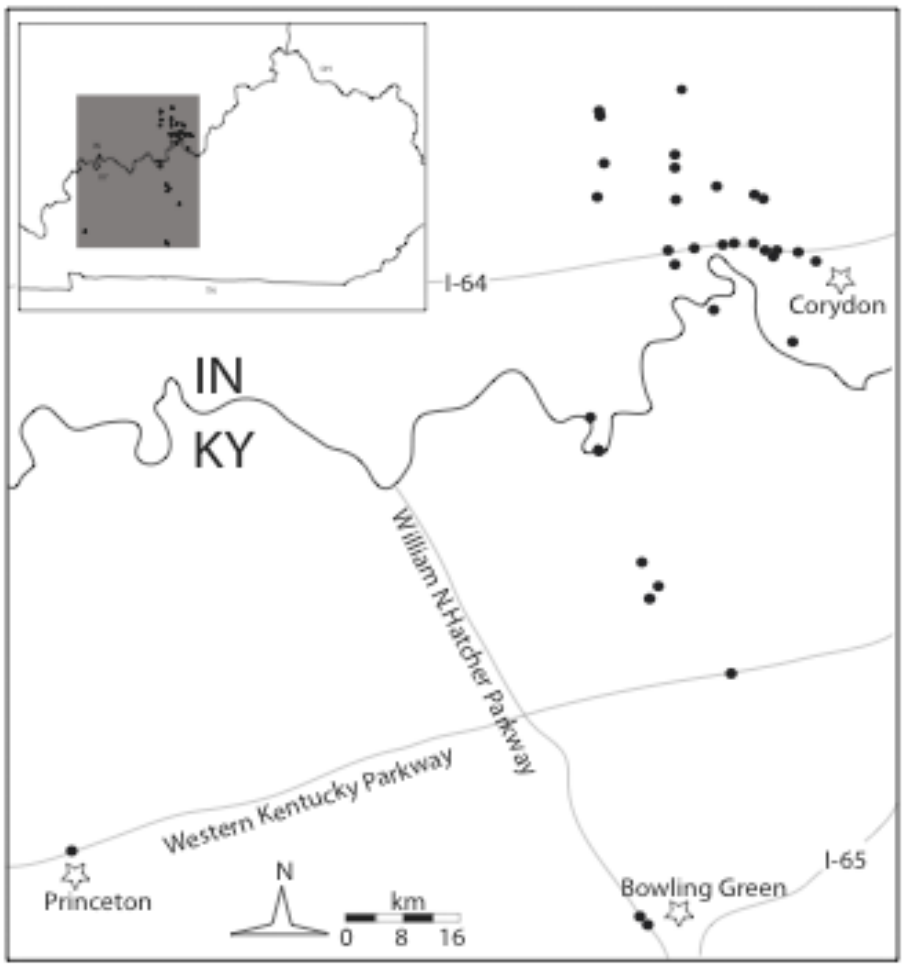
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**Figure 2.1. Map of the study area. Black circles represent sampling localities.**

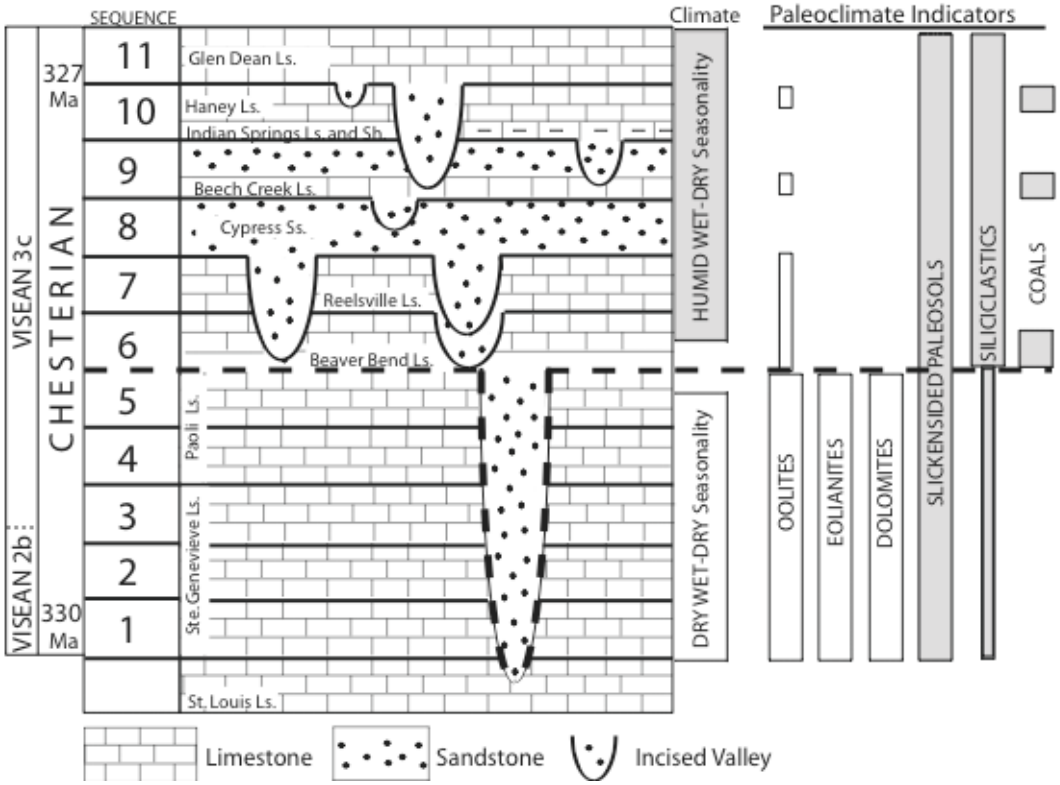



**Figure 2.2. Schematic showing depositional sequences, inferred paleoclimate, and paleoclimatic indicators for the studied interval. Bold dashed line represents the onset of the LPIA.**

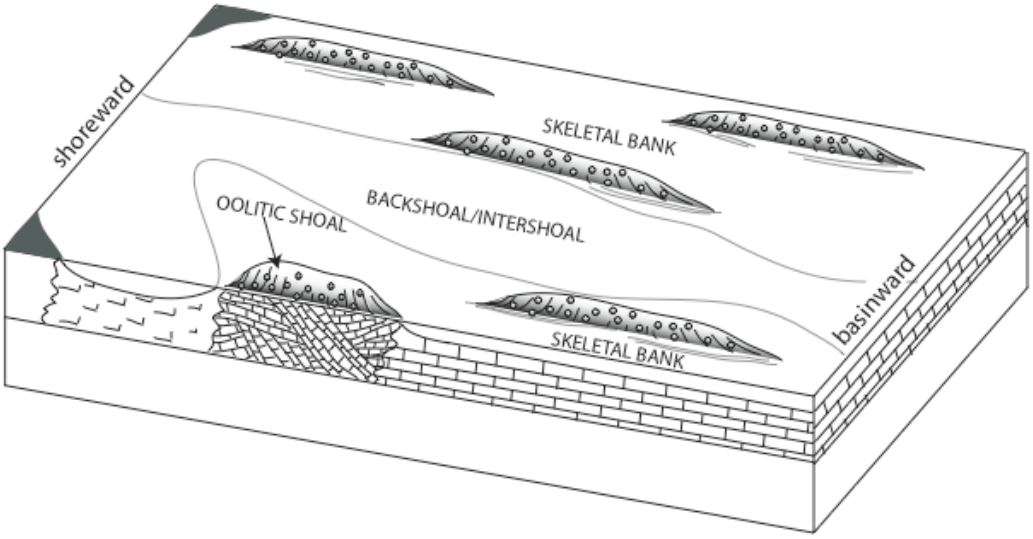



**Figure 2.3. Schematic representation of depositional environments for the pre-LPIA interval.**

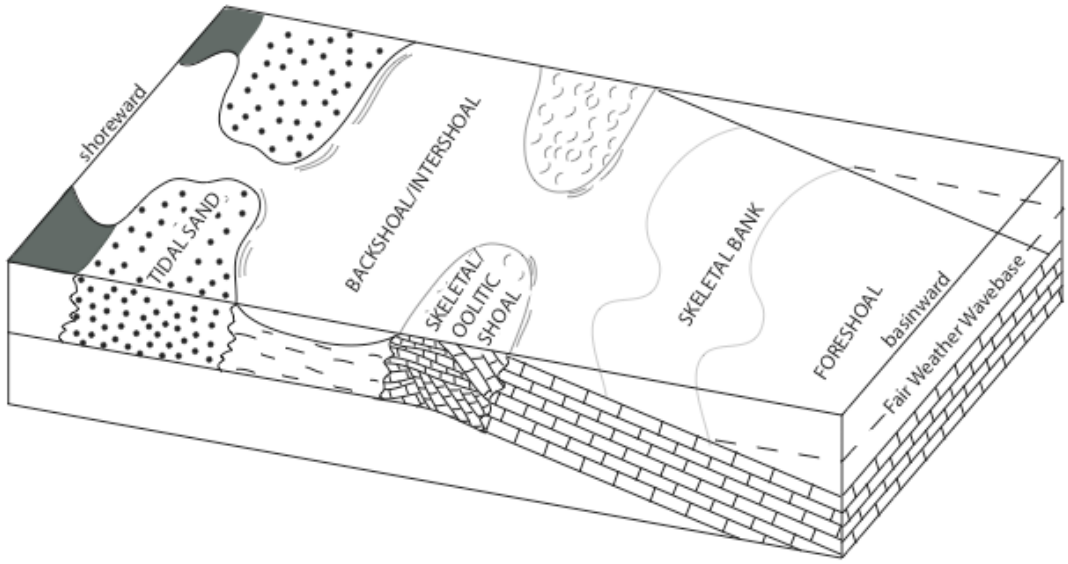



**Figure 2.4. Schematic representation of depositional environments for the LPIA interval.**

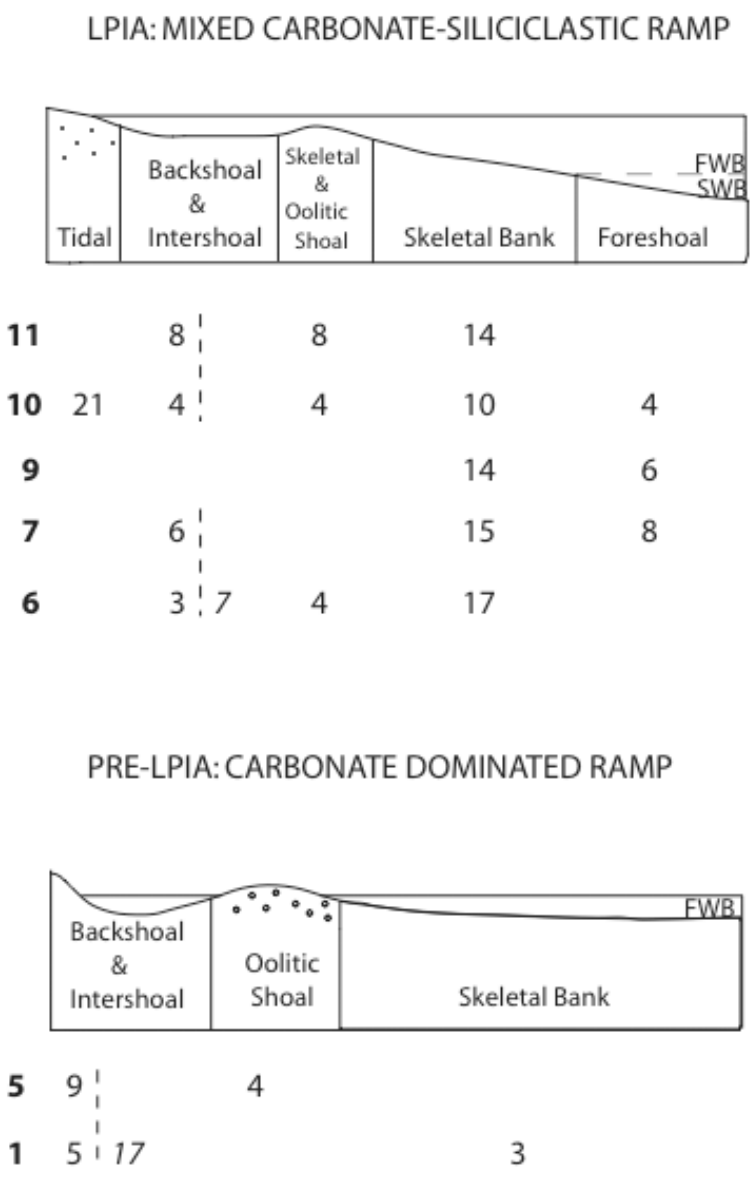



**Figure 2.5. Time-environment plot of number of samples grouped by depositional sequence and environment for the LPIA (top) and pre-LPIA (bottom) intervals. Sequence numbers appear in bold print.**

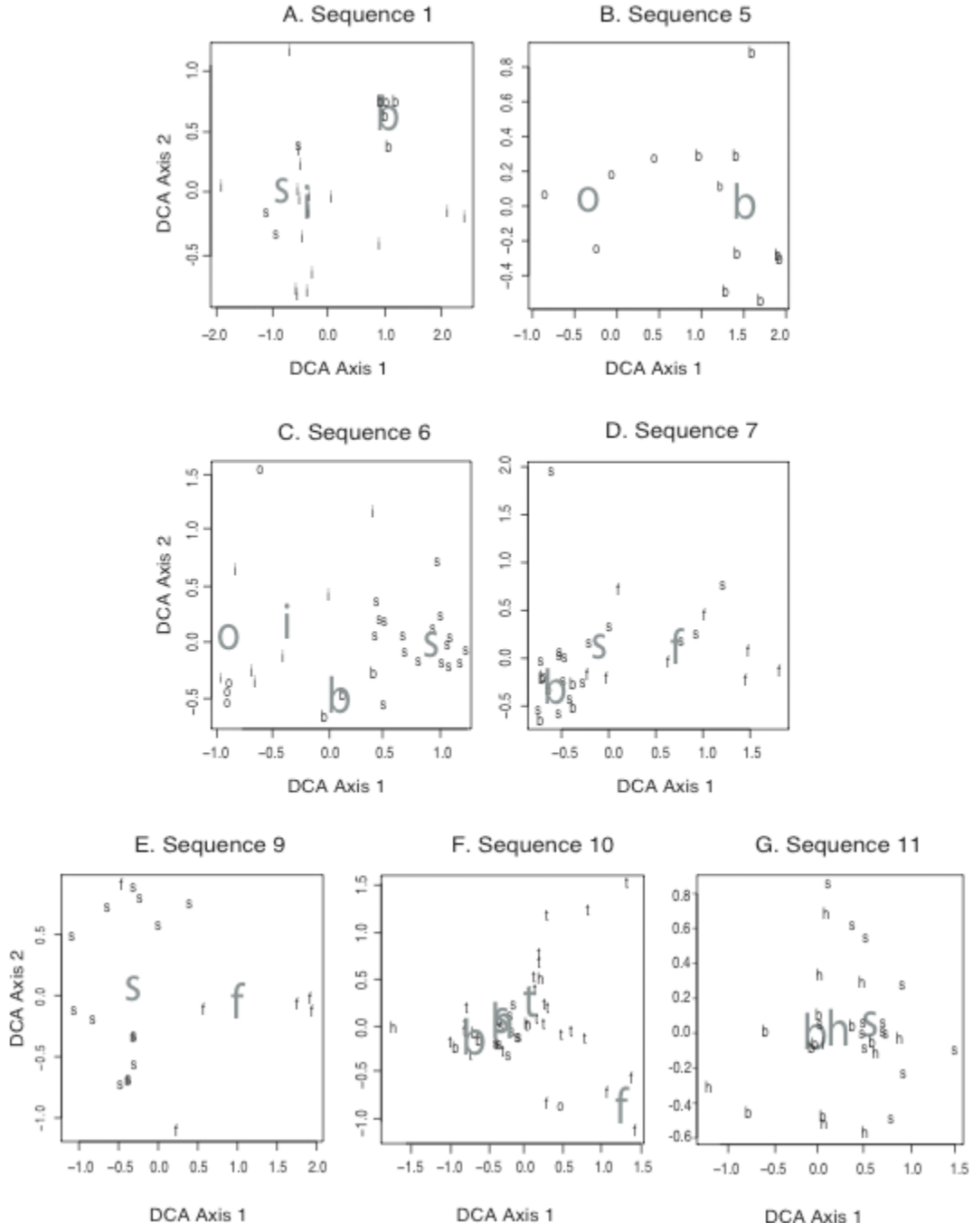



**Figure 2.6. DCA ordination results with sample scores plotted by depositional environment. A) Sequence 1. B) Sequence 5. C) Sequence 6. D) Sequence 7. E) Sequence 9. F) Sequence 10. G) Sequence 11. t = tidal flat, i = intershoal; b = backshoal; o = oolitic shoal; h = skeletal shoal; s= skeletal bank; f = foreshoal; x = sample outliers as determined in cluster analysis. Small type in plots corresponds to individual samples; large type indicates the average score of samples from a given depositional environment.**

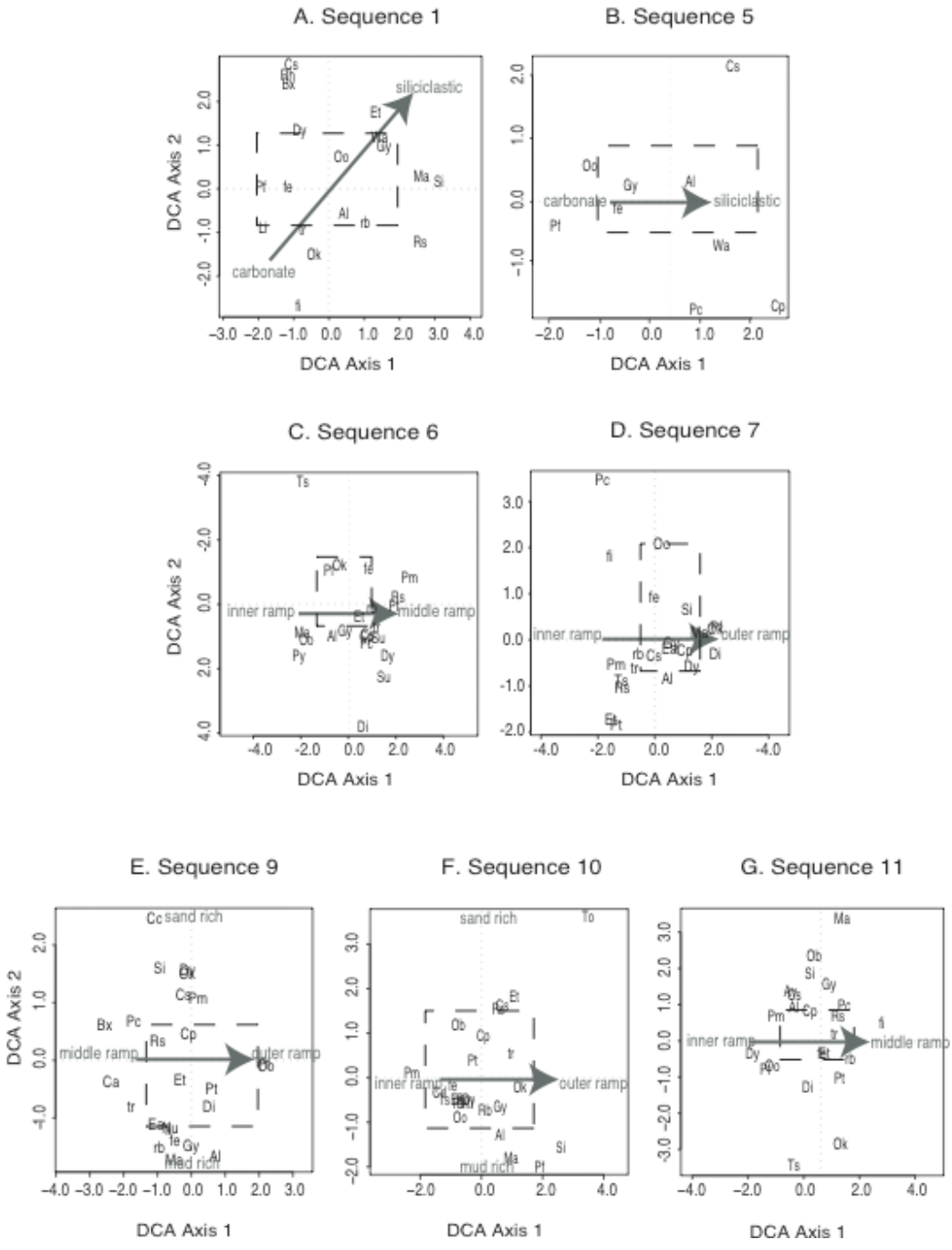



**Figure 2.7. DCA ordination results from analysis on taxa. A) Sequence 1. B) Sequence 5. C) Sequence 6. D) Sequence 7. E) Sequence 9. F) Sequence 10. G) Sequence 11. The dashed box in the plot delineates the area within which sample scores plot. Two-letter taxon codes are displayed in Table 2.1.**

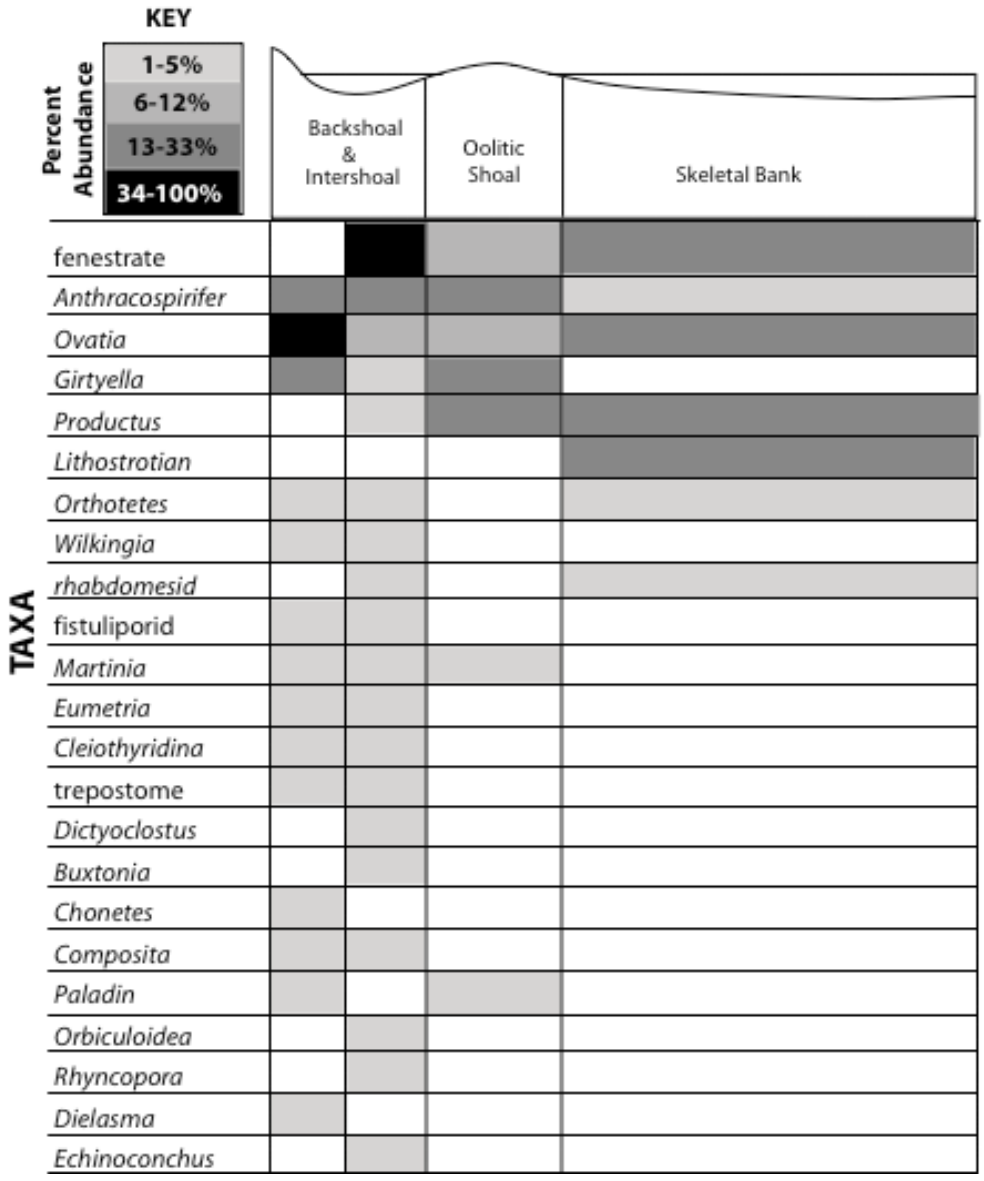



**Figure 2.8. Plot of the distribution and abundance of taxa among the depositional environments present in the pre-LPIA interval (sequences 1 and 5). Taxa are listed in rank order based upon their percent abundance.**

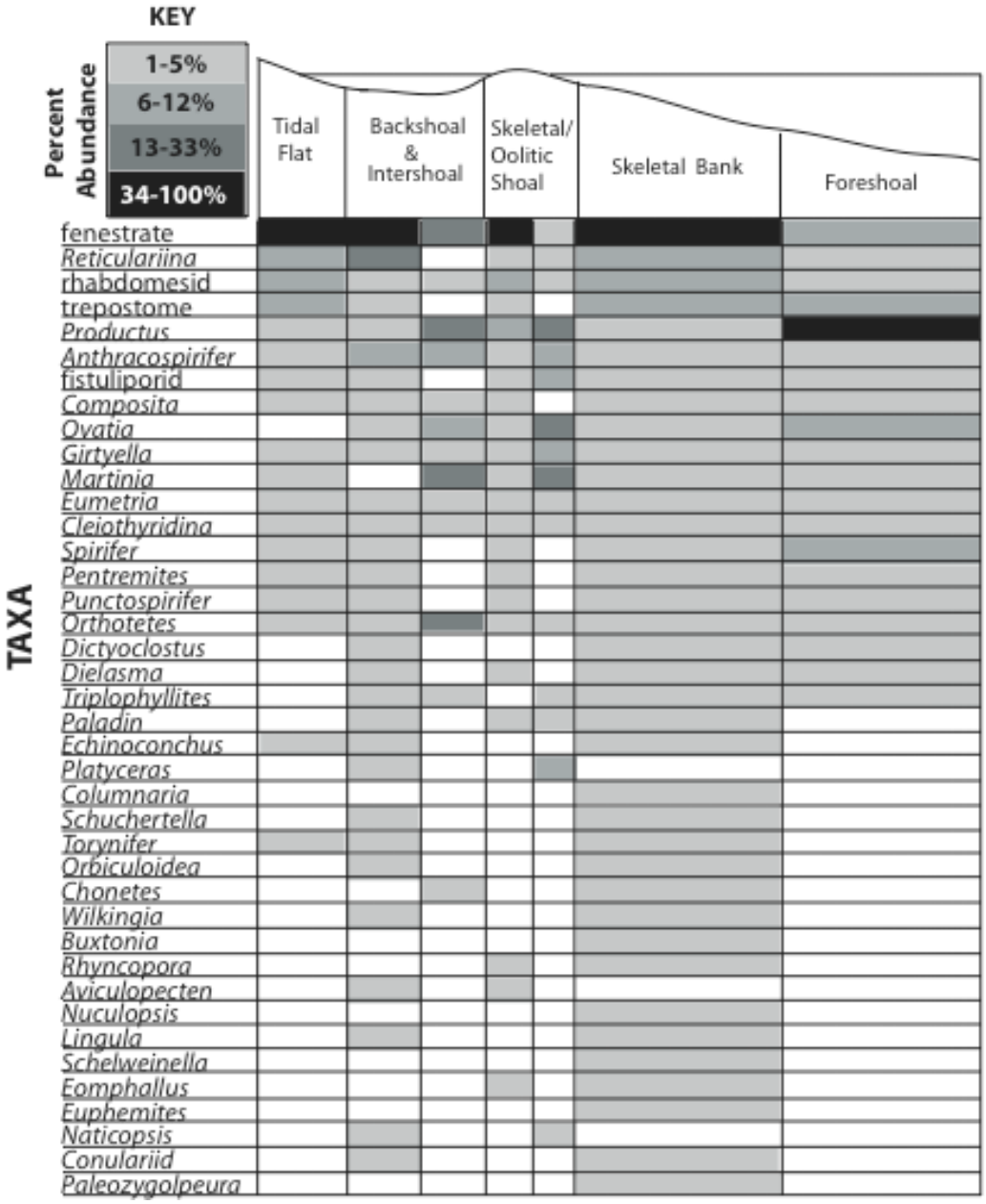



**Figure 2.9. Plot of the distribution of taxa among the depositional environments present in the LPIA interval (sequences 6-11). Taxa are listed in rank order based upon their percent abundance.**

| Code | Taxon | Code | Taxon |
|---|---|---|---|
| Al | *Anthracospirifer* (br) | Oo | *Ovatia* (br) |
| Av | *Aviculopecten* (bi) | Pa | *Paleozygolpuera* (ga) |
| Bx | *Buxtonia* (br) | Pc | *Paladin* (tr) |
| Cc | *Chonetes* (br) | Pm | *Pentremites* (bl) |
| Cs | *Cleiothyridina* (br) | Py | *Platyceras* (ga) |
| Ca | *Columnaria* (co) | Pf | *Productus* (br) |
| Cp | *Composita* (br) | Pt | *Punctospirifer* (br) |
| Cd | conularid | Rs | *Reticulariina* (br) |
| Dy | *Dictyoclostus* (br) | rb | rhabdomesid bryozoan |
| Di | *Dielasma* (br) | Ry | *Rhyncopora* (br) |
| Ea | *Echinoconchus* (br) | Su | *Schelwienella* (br) |
| Et | *Eumetria* (br) | Sc | *Schuchertella* (br) |
| Eu | *Euphamites* (ga) | Si | *Spirifer* (br) |
| Em | *Euomphalus* (ga) | To | *Torynifer* (br) |
| fe | fenestrate bryozoan | tr | trepostome bryozoan |
| fi | fistuliporid bryozoan | Ts | *Triplophyllites* (co) |
| Gy | *Girtyella* (br) | Wa | *Wilkingia* (bi) |
| Lg | *Lingula* (br) | | |
| Li | *Lithostrotian* (co) | | |
| Ma | *Martinia* (br) | | |
| Na | *Naticopsis* (ga) | | |
| Nu | *Nuculopsis* (bi) | | |
| Ob | *Orbiculoidea* (br) | | |
| Ok | *Orthotetes* (br) | | |

**Table 2.1. Taxon codes used in figure 2.7. Letters in parentheses indicate taxonomic group as follows: br = brachiopod, bi = bivalve, co = coral, ga = gastropod, tr = trilobite.**

| Backshoal | | Intershoal | | Oolitic shoal | | Skeletal bank | |
|---|---|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| *Ovatia* | 34.4 | fenestrate | 50.7 | *Productus* | 31.0 | fenestrate | 31.4 |
| *Anthracospirifer* | 26.8 | *Anthracospirifer* | 19.6 | *Girtyella* | 27.6 | *Lithostrotian* | 30.0 |
| *Girtyella* | 21.1 | *Ovatia* | 6.7 | *Anthracospirifer* | 20.7 | *Ovatia* | 17.5 |
| *Wilkingia* | 5.1 | *Productus* | 5.3 | fenestrate | 6.9 | *Productus* | 16.1 |
| *Martinia* | 3.9 | *Orthotetes* | 3.6 | *Ovatia* | 6.9 | *Anthracospirifer* | 3.6 |
| *Eumetria* | 3.0 | rhabdomesid | 3.3 | *Martinia* | 3.4 | *Orthotetes* | 0.7 |
| *Chonetes* | 1.4 | fistuliporid | 3.1 | *Paladin* | 3.4 | rhabdomesid | 0.7 |
| *Composita* | 1.0 | *Cleiothyridina* | 1.7 | | | | |
| *Orthotetes* | 0.6 | trepostome | 1.4 | | | | |
| *Cleiothyridina* | 0.6 | *Dictyoclostus* | 1.4 | | | | |
| *Paladin* | 0.6 | *Buxtonia* | 1.0 | | | | |
| *Dielasma* | 0.4 | *Girtyella* | 0.5 | | | | |
| fistuliporid | 0.2 | *Orbiculoidea* | 0.4 | | | | |
| trepostome | 0.2 | *Wilkingia* | 0.3 | | | | |
| | | *Eumetria* | 0.3 | | | | |
| | | *Rhyncopora* | 0.3 | | | | |
| | | *Martinia* | 0.1 | | | | |
| | | *Composita* | 0.1 | | | | |
| | | *Echinoconchus* | 0.1 | | | | |

**Table 2.2. Taxon Abundances by depositional environment for the pre-LPIA interval**

A.

| Sequence | *R* -value All Habitats | N |
|---|---|---|
| 11 | 0.192 | 31 |
| 10 | 0.255 | 44 |
| 9 | 0.523 | 20 |
| 7 | 0.258 | 29 |
| 6 | 0.743 | 31 |
| 5 | 0.885 | 10 |
| 1 | 0.819 | 21 |

B.

| Sequence | *R* -value All Habitats | N |
|---|---|---|
| 11 | 0.251 | 23 |
| 10 | 0.336 | 20 |
| 9 | - | - |
| 7 | 0.361 | 21 |
| 6 | 0.743 | 31 |
| 5 | 0.885 | 10 |
| 1 | 0.819 | 21 |

C.

| Sequence | *R* -value All Habitats | N |
|---|---|---|
| 11 | 0.106 | 31 |
| 10 | 0.284 | 42 |
| 9 | 0.541 | 20 |
| 7 | 0.099 | 29 |
| 6 | 0.608 | 31 |
| 5 | 0.896 | 10 |
| 1 | 0.659 | 21 |

D.

| Sequence | *R* -value All Habitats | N |
|---|---|---|
| 11 | 0.090 | 23 |
| 10 | 0.257 | 20 |
| 9 | - | - |
| 7 | 0.361 | 21 |
| 6 | 0.608 | 31 |
| 5 | 0.896 | 10 |
| 1 | 0.659 | 21 |

**Table 2.3. Results of ANOSIM tests by sequences for differentiation of faunas among environments. A) Results for tests among all the depositional environments contained within a sequence. B) Results for tests only among environments that co-occur in the pre-LPIA and LPIA intervals. C) Results for tests from part A when bryozoan taxa where removed from the analysis. D) Results for tests from part B where bryozoans were removed from the analysis. Correlation analysis of ANOSIM *R*-value as a function of the number of samples yields: r=0.22, $r^2$=0.53, *p*=0.06 for A and $r^2$=0.05, *p*=0.67 for B. Dashed line denotes onset of the LPIA.**

| Tidal | | Backshoal | | Intershoal | | Skeletal Shoal | |
|---|---|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| fenestrate | 56.7 | fenestrate | 44.9 | *Productus* | 20.1 | fenestrate | 52.3 |
| rhabdomesid | 10.8 | *Reticulariina* | 18.0 | fenestrate | 18.7 | rhadomesid | 11.8 |
| trepostome | 7.7 | *Anthracospirifer* | 9.5 | *Martinia* | 15.8 | *Productis* | 5.8 |
| *Reticulariina* | 6.4 | *Productus* | 4.1 | *Orthotetes* | 14.4 | trepostome | 4.7 |
| *Spirifer* | 3.5 | *Eumetria* | 3.8 | *Ovatia* | 9.4 | *Anthracospirif* | 4.0 |
| *Eumetria* | 3.3 | trepostome | 2.7 | *Anthracospirif* | 7.9 | *Girtyella* | 3.5 |
| fistuliporid | 3.0 | *Composita* | 2.7 | *Composita* | 3.6 | fistuliporid | 3.4 |
| *Cleiothyridina* | 1.8 | rhabdomesid | 2.6 | *Girtyella* | 2.9 | *Reticulariina* | 2.3 |
| *Pentremites* | 1.5 | *Dielasma* | 2.4 | rhabdomesid | 2.2 | *Eumetria* | 2.0 |
| *Punctospirifer* | 1.3 | fistuliporid | 2.3 | *Cleiothyridina* | 2.2 | *Ovatia* | 1.3 |
| *Productus* | 1.2 | *Cleiothyridina* | 1.4 | *Eumetria* | 0.7 | *Composita* | 1.1 |
| *Composita* | 1.1 | *Pentremites* | 1.1 | *Triplophyllites* | 0.7 | *Cleiothyridina* | 1.1 |
| *Anthracospirifer* | 0.5 | *Triplophyllites* | 0.9 | *Chonetes* | 0.7 | *Pentremites* | 1.1 |
| *Orthotetes* | 0.5 | *Ovatia* | 0.8 | | | *Paladin* | 1.1 |
| *Martinia* | 0.3 | *Girtyella* | 0.8 | | | *Spirifer* | 1.0 |
| *Torynifer* | 0.3 | *Punctospirifer* | 0.7 | | | *Orthotetes* | 1.0 |
| *Girtyella* | 0.1 | *Orthotetes* | 0.5 | | | *Martinia* | 0.9 |
| *Echinoconchus* | 0.1 | *Dictyoclostus* | 0.5 | | | *Dielasma* | 0.7 |
| | | *Toryinfer* | 0.3 | | | *Punctospirifer* | 0.3 |
| | | *Paladin* | 0.2 | | | *Aviculopecten* | 0.3 |
| | | *Platyceras* | 0.1 | | | *Rhyncopora* | 0.1 |
| | | *Spirifer* | <0.1 | | | *Euomphalus* | 0.1 |
| | | *Echinoconchus* | <0.1 | | | | |
| | | *Schuchertella* | <0.1 | | | | |
| | | *Orbiculoidea* | <0.1 | | | | |
| | | *Wilkingia* | <0.1 | | | | |
| | | *Aviculopecten* | <0.1 | | | | |
| | | *Lingula* | <0.1 | | | | |
| | | *Naticopsis* | <0.1 | | | | |
| | | *Comulariid* | <0.2 | | | | |

**Table 2.4. Taxon abundances by depositional environment for the LPIA interval (continued on next page).**

| Oolitic Shoal | | Skeletal Bank | | Foreshoal | |
|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| *Productus* | 23.1 | fenestrate | 41.2 | *Productus* | 37.5 |
| *Martinia* | 17.9 | rhabdomesid | 10.3 | *Ovatia* | 12.1 |
| *Ovatia* | 16.1 | trepostome | 8.7 | fenestrate | 11.2 |
| *Platyceras* | 12.2 | *Reticulariina* | 6.4 | trepostome | 9.6 |
| *Anthracospirfer* | 6.4 | fistuliporid | 4.0 | *Spirifer* | 5.5 |
| *Girtyella* | 6.4 | *Composita* | 3.9 | *Dictyoclostus* | 5.3 |
| rhabdomesid | 4.5 | *Productus* | 3.3 | *Martinia* | 4.8 |
| *Orthotetes* | 3.8 | *Girtyella* | 2.8 | *Composita* | 2.4 |
| fenestrate | 3.2 | *Martinia* | 2.3 | *Girtyella* | 2.3 |
| fistulipord | 1.9 | *Cleiothyridina* | 2.1 | *Anthracospirifer* | 1.9 |
| *Cleiothyridina* | 1.3 | *Pentremites* | 1.9 | rhabdomesid | 1.6 |
| *Reticulariina* | 0.6 | *Eumetria* | 1.8 | *Reticulariina* | 1.3 |
| *Eumetria* | 0.6 | *Punctospirifer* | 1.7 | *Dielasma* | 1.3 |
| *Triplophyllites* | 0.6 | *Anthracospirifer* | 1.7 | *Orthotetes* | 0.7 |
| *Paladin* | 0.6 | *Ovatia* | 1.2 | *Punctospirifer* | 0.6 |
| *Naticopsis* | 0.6 | *Spirifer* | 1.1 | *Eumetria* | 0.4 |
| | | *Orthotetes* | 1.0 | *Cleiothyridina* | 0.3 |
| | | *Dictyoclostus* | 0.9 | *Pentremites* | 0.3 |
| | | *Triplophyllites* | 0.7 | fistuliporid | 0.1 |
| | | *Echinoconchus* | 0.5 | *Triplophyllites* | 0.1 |
| | | *Dielasma* | 0.5 | | |
| | | *Paladin* | 0.4 | | |
| | | *Columnaria* | 0.3 | | |
| | | *Schuchertella* | 0.2 | | |
| | | *Orbiculoidea* | <0.1 | | |
| | | *Chonetes* | <0.1 | | |
| | | *Wilkingia* | <0.1 | | |
| | | *Buxtonia* | <0.1 | | |
| | | *Rhyncopora* | <0.1 | | |
| | | *Nuculopsis* | <0.1 | | |
| | | *Toryinfer* | <0.1 | | |
| | | *Schellwienella* | <0.1 | | |
| | | *Euphemites* | <0.1 | | |
| | | *Lingula* | <0.1 | | |
| | | *Euomphalus* | <0.1 | | |
| | | *Conulariid* | <0.1 | | |
| | | *Paleozygopluera* | <0.1 | | |

**Table 2.4. Continued from last page.**

# Chapter 3. Taxonomic and Ecologic Stability During the Late Paleozoic Ice Age: Evidence from the Upper Mississippian (Chesterian Series) Illinois Basin, USA

## Introduction

The interval of massive continental glaciation that occurred from the latest Mississippian to the early Permian, commonly referred to as the late Paleozoic ice age (LPIA), coincided with a significant restructuring of the global marine ecosystem. For example, the onset of the LPIA was accompanied by a 28% reduction of global marine generic diversity (a second order mass extinction) and was followed by an abrupt decline in rates of both origination and extinction (Stanley and Powell 2003, Stanley 2007). The very protracted rebound (approximately 50 Myr) of diversity and taxonomic rates from this biotic crisis contrasts greatly with the rapid recoveries that follow all other Paleozoic mass extinctions (Hallam and Wignall 1997, Stanley and Powell 2003, Stanley 2007). In addition, it has been shown that climate changes associated with the LPIA altered the biogeographic structure of marine faunas by preferentially eliminating narrowly distributed tropical genera (Powell 2005, 2007); this caused the latitudinal gradient of biotic diversity to become distinctly lower during the LPIA, relative to intervals before and after the ice age (Powell 2005, 2007). Despite these significant global-level biotic changes, major questions remain concerning how these patterns are manifest at the more local level of communities or regional ecosystems; these include: (1) do regional and local patterns of diversity change and turnover reflect the global pattern during and after the onset of the LPIA? (2) How did the ecological structure (i.e., guild diversity and

dominance) of marine assemblages respond to the significant global diversity and environmental changes that occurred during the LPIA?

We address these questions using a dataset that was collected from the Chesterian Series (Upper Mississippian) of the Illinois Basin region (Kentucky and Indiana). The Chesterian Series of the Illinois Basin encompasses approximately 4 Myr and spans the onset and early phases of the LPIA (Smith and Read 2000). This succession has been placed within a well resolved environmental and sequence stratigraphic framework of 11 high frequency (~300-450 Kyr) depositional sequences (Smith and Read 1999, 2001, Nelson et al. 2002), which makes it an ideal setting for examining local and regional diversity and guild patterns at a relatively high temporal resolution. Although the Chesterian Series is richly fossiliferous and has been taxonomically well studied (Weller 1916, Weller 1931, 1936, Sutton 1938a, McFarlan 1942, Haas 1945, Batchelor 1948, Brookley 1955, Horowitz 1956, Rodriguez 1960, Perry and Horowitz 1963, Horowitz 1965, Thein and Nitecki 1974, Chestnut and Ettensohn 1988, Rexroad 1992), there have been no quantitative examinations of the taxonomic or guild diversity of its fauna as a whole, or in response to environmental changes associated with the LPIA; however, the paleoecology of some individual stratigraphic intervals has been studied (see Vincent 1975, Kelly 1984).

In this chapter we present rarefaction and faunal turnover analyses of the brachiopod and bryozoan dominated communities that are preserved within seven fourth-order depositional sequences (~350-400 Kyr each) from the Chesterian Series of the Illinois Basin. These analyses are used to describe and compare taxonomic and guild diversity at many levels: (1) through time- among depositional sequences deposited

before and during the LPIA; (2) through space- among the habitats that comprise the regional ecosystems preserved within each depositional sequence; and (3) within an environment, through cycles of glacio-eustasy. We use these results to understand how the global diversity and environmental changes that took place in the early LPIA are reflected in the diversity and guild structures of assemblages at the local and regional levels.

## Geologic Background

The Chesterian Series of the Illinois Basin region is well exposed across Indiana and Kentucky. In this study, we use a data set derived from 33 sampling localities that consist mostly of road-cuts and natural exposures (Fig. 3.1, Appendix B). During the Chesterian, the Illinois Basin was situated within a tropical setting, between 5˚ and 15˚ south of the equator and comprised part of a widespread, shallow carbonate ramp that extended into western Canada (Craig and Connor 1979, Scotese and McKerrow 1990). The Chesterian strata in the study area can be subdivided into two intervals: (1) pre-LPIA strata are comprised of sequences 1-5; (2) LPIA strata include sequences 6-11 (Fig. 3.2). The inferred onset of the LPIA occurs at the sequence bounding unconformity at the base of sequence 6 (Fig. 3.2). This unconformity represents the first occurrence of a deeply incised valley in the study interval and has been interpreted to reflect eustatic sea level fall associated with the first major pulse of ice growth during the LPIA, on the southern continent of Gondwana (Smith and Read 2001).

**Pre-LPIA Interval**

Pre-LPIA sequences developed on a very gently sloping (< 5 cm/km), carbonate-dominated ramp (Smith and Read 1999). Because these sequences lack deeply incised valleys and significant subaerial exposure surfaces, they are thought to have been produced by moderate amplitude (10-30 m), eustatic sea level fluctuations just prior to the onset of the LPIA (Fig. 3.2; Smith and Read 1999). Local tidal energy, rather than water depth, controlled facies distribution along the pre-LPIA ramp and created a mosaic of habitats oriented in dip, rather than strike, parallel belts (Smith and Read 1999).

The pre-LPIA interval contains four fossiliferous marine lithofacies: backshoal, intershoal, oolitic shoal, and skeletal bank (see Hunter 1993, Smith and Read 1999, Dodd et al. 2001). The backshoal facies, a siliciclastic facies, is exceedingly rare in the pre-LPIA interval, but was sampled where present; it is dominantly fissile, olive green to dark grey fossiliferous shale that may be interbedded with wackestone and packstone; it represents deposition in protected, shallow water, low energy settings behind oolitic shoals, during infrequent periods of siliciclastic influx (Smith and Read 1999). The intershoal consists of light grey to tan, massive, sparsely fossiliferous lime mudstones and wackestones that represent low energy carbonate muds deposited in-between and updip of oolitic shoals (Carr 1973, Hunter 1993, Smith and Read 1999). The oolitic shoal facies is white to light gray, massive to cross and planar-bedded, skeletal, oolitic grainstones, which were deposited in high energy, shallow marine settings (Carr 1973, Smith and Read 1999, 2001). The skeletal bank is dominated by light to dark gray, thick to medium and sometimes cross-bedded skeletal grainstones and packstones that were deposited in

shallow water (< 10 m), medium to high-energy settings landward, in between, and seaward of oolitic shoals (Smith and Read 1999).

**LPIA Interval**

The LPIA sequences differ in nature from those of the pre-LPIA interval. First, LPIA sequences preserve deeply incised valleys and extensive exposure surfaces, which are thought to reflect periods of significant Gondwanan ice build up and associated base-level fall – up to 95 m (Fig. 3.2; Smith and Read 1999, 2000, 2001). Second, these sequences were deposited on a more steeply dipping (< 7 cm/km), tidal and storm influenced ramp and display facies belts that are oriented strike parallel and change down dip in response to increasing water depth (Smith and Read 2001). In addition, siliciclastic lithofacies are more common and comprise an important component of all depositional sequences in the LPIA interval.

Seven fossiliferous marine lithofacies comprise the LPIA sequences: tidal flat, backshoal/intershoal, skeletal-oolitic shoal, skeletal bank, and foreshoal (Smith and Read 2001). The tidal flat facies consists of orange to grey, very fine to medium grained, cross to massive bedded, quartz sandstone that formed in a tide dominated, shallow marine environment (Huff 1993, Smith and Read 2001, Nelson et al. 2002). The skeletal bank facies lacks the cross bedding and ooids seen in the pre-LPIA interval, but contains graded grainstone and packstone beds. These differences likely reflect a more distal ramp position and suggest greater storm influence (Smith and Read 2001). The foreshoal environment consists of medium to dark grey, thick to massive bedded, skeletal

wackestone and mudstones that were deposited above storm wave base and represent the most distal environmental sampled along the LPIA ramp (Smith and Read 2001).

## Faunal Data

The dataset for this study differs slightly from the dataset used in Chapter 2 to examine biotic gradients during the LPIA. Here, we use a larger dataset including samples that had been culled from the data set used for Chapter 2 due to their small size. We feel it is appropriate to incorporate data from these small samples because we are primarily concerned with taxonomic diversity and want to ensure that all recovered taxa are included in our analyses. All told, this dataset consists of 12,916 individuals collected from 197 fossiliferous samples.

We focus our study on seven of the eleven total depositional sequences preserved in the study interval. These seven sequences were selected because they containe easily accessible outcrops from which we could make fossil collections. In all, two pre-LPIA sequences (1 and 5) and five LPIA sequences (6, 7, 9, 10, 11) were sampled (Fig. 3.3) by collecting two to five laterally distributed bulk samples from targeted facies at each sampling locality (cf Bennington and Rutherford 1999, Bennington 2003). Samples were returned to the lab and fossil specimens were identified to the finest taxonomic level possible using the *Treatise on Invertebrate Paleontology* and taxonomic descriptions of Chesterian fossils contained in the literature (e.g., Weller 1916, Weller 1931, 1936, Sutton 1938a, McFarlan 1942, Moore 1948, Brookley 1955, Horowitz 1956, Rodriguez 1960, Perry and Horowitz 1963, Horowitz 1965, Thein and Nitecki 1974, Brezinski 1988,

Chestnut and Ettensohn 1988, Busanus and Hoare 1991, Henry and Gordon 1992, Hoare 1993). To maximize the use of as much data as possible, all of our analyses are conducted at the generic level because most specimens, other than bryozoans, could be identified to genus; bryozoan taxa were identified to family. We feel confident that increasing the taxonomic resolution of this study to species would not have changed our results because many of the identified genera were monospecific. Fossil individuals were counted using the minimum number of individuals (MNI) method, which provides a relatively conservative estimate of fossil abundances (Gilinsky and Bennington 1994). Although there is no clear way to best measure the abundance of colonial organisms, such as bryozoans and corals, relative to that of bivalved taxa, we counted each 1 cm length of colony as one individual (see also Patzkowsky and Holland 1999, Holland and Patzkowsky 2004); in this way we could assess the importance of colonial taxa and their respective guilds within our data set. In all, 48 taxa (including brachiopods, bivalves, gastropods, bryozoans, blastoids, corals, and trilobites ) were recovered from our samples, which had a mean size of 65.6 individuals and median size of 50.0 individuals.

## Quantitative Methods

Analytic rarefaction (Hurlbert 1971, Simberloff 1972, Heck et al. 1975, Raup 1975, Tipper 1979) was used to estimate and compare generic or guild diversity among depositional sequences or environments. Rarefaction analysis permits the numerical estimation of taxonomic richness at sub-sample sizes that are smaller than the size of the original collections. Rarefaction curves are plotted against the size of the sub-sample and

can facilitate a comparison of taxonomic richness among collections of different sizes. To conduct rarefaction analyses, we first created data files containing the abundances of taxa that were collected from the sequences or habitats of interest and then performed analytic rarefaction on each data file using the software Analytic Rarefaction v. 1.3, which is available at Steve Holland's website (www.uga.edu/strata/software/index.html).

We use the Jaccard Coefficient ($S_j$) on presence-absence data to quantify compositional turnover between sequences and depositional environments. The Jaccard Coefficient (Jaccard 1908), also referred to as the "Coefficient of Community" (Sepkoski 1988), measures the proportion of taxa shared between two samples using the following formula:

$$S_j = \frac{T_C}{T_1 + T_2 - T_C}$$

where $T_1$ is the number of taxa in sample 1, $T_2$ is the number of taxa in sample 2, and $T_C$ is the number of taxa shared between the two samples. The Jaccard Coefficient ranges from 0 to 1 and is an inverse measurement of taxonomic turnover. For example, comparisons between taxonomically similar samples would produce coefficient values closer to 1 (suggesting low turnover), while compositionally dissimilar samples would yield values closer to 0 (indicating high turnover). In addition, we also calculated percent carryover and holdover metrics (see Brett and Baird 1995) as an additional measure of taxonomic turnover between sequences or depositional environments. Thus, the percent carryover metric was computed by dividing the number of taxa that persist from one sequence, lets say sequence A, into the next the sequence (sequence B) by the total number of taxa present in sequence A. In this way, the percent carryover metric

represents the proportion of taxa that persist from one sequence into the next. On the other hand, the percent holdover metric is calculated by dividing the total number of taxa that "carryover" from sequence A by the total number of taxa present in sequence B. In this way, the percent holdover metric represents the total percentage of the fauna in the subsequent sequence that is comprised of taxa from the preceding sequence.

## Results

### Regional Level Analyses: Depositional Sequences

Raw Per-Sequence Diversity

Raw total diversity per-sequence, or regional diversity, was calculated by simply adding up the total number of taxa that were recovered from a depositional sequence. Raw per-sequence diversity decreases from 25 taxa in sequence 1 to 13 taxa by sequence 5 (Fig. 3.4). Diversity more than doubles across the onset of the LPIA to 27 taxa in sequence 6 and then drops slightly to 25 taxa by sequence 7. Diversity increases to 36 taxa in sequence 9, but then decreases and remains mostly constant across sequences 10 and 11 (28 and 29 taxa, respectively). Given that the number of samples varies from sequence to sequence and that the environmental coverage of sampling differs due to increased habitat heterogeneity in the LPIA interval (see Fig. 3.3), the pattern of raw per-sequence diversity change should not be taken at face value. Numerous studies have noted a strong correlation between diversity and measures of sampling intensity (Raup 1972, 1976a, 1976b, Miller and Foote 1996, Alroy et al. 2001, Peters and Foote 2001, Smith et al. 2001a, Peters and Foote 2002, Smith 2003, Krug and Patzkowsky 2004, Smith 2007, Smith and McGowan 2007). To measure the strength of the association

between sampling intensity and per-sequence diversity in our data set, we performed a correlation analysis (see Sokal and Rohlf 1969). This analysis indicates that raw diversity is weakly associated with both the total number of samples collected for each sequence ($r = 0.39$; $r^2 = 0.15$; $p = 0.38$) and the total number of individuals recovered from each sequence ($r=0.46$; $r^2 = 0.21$; $p = 0.29$), although neither of these relationships was statistically significant.

Rarefied Per-Sequence Diversity

To account for any potential bias that may have resulted from the weak association between sampling intensity and raw taxonomic diversity, rarefaction analyses were performed (Fig. 3.5A). The results of the rarefaction analysis match well with those derived from the analysis of raw data - there is a high level of correspondence between raw and rarefied levels of per sequence diversity and in the overall pattern and magnitude of diversity change through the study interval (see Fig. 3.5B). Unfortunately, because sequence 5 was sampled at a low intensity, its diversity could not be assessed at a sample size that was comparable to all other sequences (i.e., 1000 individuals). The steep shape of the sequence 5-rarefaction curve indicates that numerous other species would likely be captured with increased sampling; for this reason we do not consider diversity relationships between sequence 5 and other sequences in this and other analyses to be meaningful. The results for remaining sequences however, show that mean per-sequence diversity changed little throughout the majority of the 4 My study interval: at a sub-sample size of 1000 individuals, the mean richness of sequences 1, 6, 7, 10, and 11 deviates only slightly, but not significantly, from a minimum of 22.9 taxa to a maximum

of 25 taxa. However, the significant increase in the taxonomic richness of sequence 9 that was shown in the raw pattern is still apparent in the rarefied data.

Diversity Turnover

We used the Jaccard Coefficient and simple percent carryover and holdover metrics to examine whether any major compositional changes might have occurred from sequence-to-sequence or across the onset of the LPIA, even though we failed to observe major diversity changes throughout much of the study interval (Table 3.1A). Not surprisingly, the greatest sequence-to-sequence turnover was measured between sequences 1 and 5 ($S_j$ = 0.46) and between sequences 5 and 6 ($S_j$ = 0.43). Again, we attribute this result to the low sampling intensity of sequence 5: given its small total sample size we would expect that sequence 5 could be missing a number of common and rare taxa from its genus roster, thus elevating turnover in comparisons between it and any other sequence. Lower levels of turnover, ranging from 0.56 to 0.78, were measured for all of the comparisons involving the LPIA sequences. Percent carryover and holdover metrics indicate that anywhere from 63.8% to 89.2% of taxa were found to persist from one LPIA sequence to the next (see Table 3.1); furthermore, these "carryover taxa" typically comprise 61.1% to 88.0% of the total pool of species in the ensuing sequence. Taken together, these data suggest that in addition to the lack of per sequence diversity change, very low levels of turnover characterize the LPIA sequences.

In an attempt to gauge turnover between the pre-LPIA and LPIA intervals, we made some additional comparisons between sequence 1 and each LPIA sequence (Table 3.1B). Although our pre-LPIA data are limited in quantity, sequence 1 was sampled to a

comparable degree as the LPIA sequences and should serve as an adequate data point for comparison. Perhaps surprisingly, the level of turnover exhibited among sequence 1 and each LPIA sequence was relatively low ($S_j$ = 0.59 to 0.63; percent carryover = 76% to 92%; percent holdeover = 63.9% to 76%) and fell well within the range of turnover displayed between typical LPIA sequences (see Table 3.1B). These results suggests that the turnover of diversity between the pre-LPIA sequence (sequence 1) and LPIA sequences may have been no greater than that between LPIA sequences.

**Local Level Analysis: Depositional Environments**

Habitat Diversity

We limit our analysis of depositional environments to the backshoal, skeletal bank, and foreshoal habitats because these are the most intensely sampled environments and, with the exception of the foreshoal, occur in both the pre-LPIA (sequence 1) and the LPIA sequences. Rarefaction results suggest that diversity relationships among habitats vary from sequence to sequence (Fig. 3.6 A-E). For example, the diversity of the skeletal bank environment is significantly higher than the backshoal and/or foreshoal in two of the five LPIA sequences- sequences 6 and 9 (Fig. 3.6 A, C). However, in sequence 7 the diversity of the skeletal bank and foreshoal environments are indistinguishable from one another, but significantly greater than the backshoal habitat at a sub-sample size of 400 individuals (Fig. 3.6B). In sequence 10, the mean diversity of the backshoal, skeletal bank, and foreshoal habitats cannot be differentiated when examined at a standardized sample size of 160 individuals (the sample size of the backshoal habitat) (Fig. 3.6D); likewise, when compared at 1000 individuals, the diversity of the skeletal bank and

foreshoal habitats still cannot be distinguished from one another. Unlike the other LPIA sequences, the greatest habitat diversity resides in the backshoal in sequence 11; when compared at 1200 individuals, the backshoal environment has significantly higher diversity than the skeletal bank environment (Fig. 3.6E).

Diversity Turnover

Using the Jaccard Coefficient we measured turnover between (1) the backshoal and skeletal bank environments and (2) the skeletal bank and foreshoal environments at the sequence-by-sequence level (Table 3.2). The greatest turnover between the backshoal and skeletal bank habitats was measured for sequence 1 ($S_j$ = 0.18); however, this result may reflect poor sampling because only three samples were collected from the skeletal bank environment from sequence 1. It is likely that, with only three samples, we did not recover every taxon that inhabited this environment and may be missing some common and/or rare taxa. The LPIA sequences however, displayed lower levels of turnover between environments: turnover between the backshoal and skeletal bank habitats was greater during sequence 6 ($S_j$ = 0.44) than it was for any other LPIA sequence. Relatively lower and constant levels of turnover were recorded between these two environments for sequences 7, 10, and 11 ($S_j$ = 0.74; $S_j$ = 0.67; $S_j$ = 0.74, respectively). Measured turnover between the skeletal bank and foreshoal habitats is relatively low during sequence 7 ($S_j$ = 0.73), but greater during sequences 9 and 10 ($S_j$ = 0.44 and $S_j$ = 0.46, respectively), although this particular pattern may also be associated with differences in the number of samples collected between the skeletal bank and foreshoal for sequence 9. However, correlation analysis suggests that turnover is not significantly associated with the number

of samples available for use in comparisons of the backshoal with skeletal bank ($r$ = 0.75; $r^2$ = 0.57; $p$ = 0.17) and the skeletal bank with the foreshoal ($r$ = 0.70; $r^2$ = 0.50; $p$ = 0.49). Thus, our measurements of turnover between environments are likely robust to the vagaries of sampling. These results indicate that levels of taxonomic turnover between environments remained mostly constant across depositional sequences during the LPIA study interval.

Within Habitat Diversity

Here, we compare only the diversity of the skeletal bank environment through the LPIA study interval because the skeletal bank habitat was intensely sampled in the LPIA sequences, but poorly sampled in the pre-LPIA (sequence 1). Thus, the purpose of this section is to understand how the taxonomic diversity and composition of the skeletal bank fauna varied through cycles of eustatic change during the LPIA interval only.

Rarefaction analyses show that the diversity of the skeletal bank fauna fluctuated slightly during the LPIA interval at a sub-sample size of 800 individuals (Fig. 3.7). In sequences 6 and 7 taxonomic diversity remained essentially flat and ranged from 22.4 to 22.5 taxa respectively. However, diversity increased significantly to 35.6 taxa in sequence 9. Importantly, this diversity increase is not associated with an increase in sampling intensity; rather, fewer samples were collected from the sequence 9 skeletal bank habitat than in three of the four remaining LPIA sequences (see Fig. 3.3). Following this increase, diversity then falls to 22.7 taxa in sequence 10 and continues to decrease significantly to 19.4 taxa in sequence 11.

Table 3.3 displays the results from analyses of taxonomic turnover between the LPIA skeletal bank faunas. Results indicate that turnover was relatively low among skeletal bank assemblages ($S_j$ = 0.5 to $S_j$ = 0.81) and that 55.5% to 95.6% of taxa persisted from one sequence to the next. Not surprisingly, the highest levels of taxonomic turnover occurred between sequences 9 and 10 ($S_j$ = 0.50; percent carryover = 55.5%) and can likely be attributed to the significantly greater diversity of the sequence 9 skeletal bank fauna (see Fig. 3.7). Indeed, 14 new taxa appear in the skeletal bank habitat of sequence 9, although these taxa tend to be rare and account for less than 7% (53 of 844 individuals) of the total individuals collected from the habitat overall. These rare taxa include four brachiopods (*Chonetes*, *Buxtonia*, *Rhyncopora*, and *Athyris*), two bivalves (*Nuculopsis* and *Wilkingia*), six gastropods (*Euomphalus*, *Euphemites*, *Globozyga*, *Naticopsis*, *Paleozygolpeura*, and *Trepospira*), one nautiloid (*Orthoceras*), and one colonial coral (*Columnaria*). Of these, seven taxa, *Athyris*, *Nuculopsis*, *Globozyga*, *Paleozygolpeura*, *Trepospira*, *Orthoceras*, and *Columnaria* are unique to the skeletal bank of sequence 9, and are not found in any other habitat or sequence in the study interval.

**Guild Level Analysis**

The analysis of ecological guilds provides a way in which paleoecologists can characterize the ecological complexity of fossil assemblages and measure paleoecological change associated with environmental or biological perturbations (Droser et al. 1997, Bottjer et al. 2001). Guilds represent groups of taxa with similar modes of life and feeding strategies (Bambach 1983, Dodd and Stanton 1990). Here we follow the guild

classification scheme of Bambach (1983), which uses three parameters to define ecospace: morphology, mode of life, and feeding strategy. In all, we recognize 15 separate guilds (see Table 3.4), however, most taxa were assigned to one of three major guilds: (1) pedunculate epifaunal suspension feeders (PESF)– this included all non-strophomenid and non-lingulid brachiopods; (2) reclining epifaunal suspension feeders (RESF)- all strophomenid brachiopods; and (3) sessile colonial suspension feeders (SCSF)- the fenestrate, rhabdomesid, and trepostome bryozoans. All other taxa were placed within one of 12 minor guilds: colonial microcarnivores, encrusting colonial suspension feeders, encrusting epifaunal suspension feeders, epibyssate suspension feeders, infaunal deposit feeders, mobile epifaunal parasites, mobile epifaunal scavengers, mobile grazers, nektonic carnivores, pedunculate infaunal suspension feeders, solitary attached suspension feeders, and solitary microcarnivores. These minor guilds tended to be comprised of fewer than three members (see Table 3.4).

Per-Sequence Guild Diversity

Guild diversity remains relatively unchanged throughout the Chesterian study interval, varying only from 8 to 11 guilds (Fig. 3.8). Correlation analysis indicates that raw per sequence guild diversity is weakly, but not significantly, correlated with the number of samples collected per sequence ($r$=0.51; $r^2$=0.26; $p$=0.24) and the number of individuals per sequence ($r$=0.73; $r^2$=0.54; $p$=0.06). Results from analytic rarefaction based upon individuals in each guild (Fig. 3.9) show that when sampling differences are accounted for, the total guild diversity of most sequences is still not significantly different at a sampling intensity of 1000 individuals: the confidence intervals of sequences 1, 6, 7,

10, and 11 all overlap the mean guild diversities of the other sequences. However, the guild diversity of sequence 9 is significantly greater than sequences 1, 6, 7, and 10.

Within Guild Diversity

The total number of taxa comprising each guild, which we refer to as the diversity within guilds, stays mostly constant between depositional sequences (Fig. 3.10). Sequences tend to contain a high diversity of taxa that comprise the pedunculate epifaunal suspension feeding guild (10, 11, 10, 13, 9, and 11 taxa respectively for sequences 1, 6, 7, 9, 10, and 11), followed by the reclining epifaunal guild (7, 6, 6, 8, 5, 4 taxa respectively); all other guilds contain relatively few taxa. To be fair, the diversity of the colonial suspension feeding guild in each sequence is conservatively low because it is comprised solely of bryozoan taxa, which, unlike other taxa, were identified only to the family, not genus, level.

Guild Abundance

When the relative abundance of guilds is plotted through time (Fig. 3.11) two details become apparent: (1) guild structure varies to a greater degree than per sequence guild diversity and within guild diversity; and (2) guilds that are comprised of many taxa are not always the most numerically important guilds in a sequence (i.e. they may contain few individuals). For example, though it was comprised of the greatest number of taxa, the pedunculate epifaunal suspension feeding guild (see Fig. 3.10) was dominant in only two sequences, 7 and 9, where its taxa accounted for approximately 40 % of the total number of individuals collected. In the remaining sequences, the abundance of

pedunculate epifaunal suspenion feeders is reduced by as much as 30%. The second most diverse guild, the reclining epifaunal suspension feeding guild, was of secondary or tertiary importance in most sequences and never comprised more than 34% of the total individuals collected. On the other hand, the sessile colonial suspension feeding guild was the dominant guild in sequences 1, 6, 10, and 11 and accounted for anywhere between 25-75% of the total number of individuals collected from a sequence. The 12 remaining minor guilds accounted for less than 3% of the individuals recovered from any one sequence.

## Discussion

### Linking Global and Regional Diversity Patterns Across the Onset of the LPIA

As noted previously, the onset of the LPIA is associated with major perturbations to the marine biosphere, including a 28% decrease in the global diversity of marine invertebrate genera (Stanley and Powell 2003). Given the magnitude of this extinction event, and the fact that stenotopic tropical taxa were hit especially hard (Powell 2005, 2007), we expected regional diversity in the LPIA interval to be significantly lower than diversity of the pre-LPIA interval. However, our results for regional (per-sequence) diversity through the onset of the LPIA stand in marked contrast to the global pattern of diversity. For example, per sequence taxonomic diversity remains fairly constant in the Illinois Basin among sequence 1 (pre-LPIA) and four of the five LPIA sequences (see Fig. 3.5A). We have also shown that there is very little faunal turnover between the pre-LPIA and LPIA intervals on the whole and that the turnover that did occur was certainly no greater than that displayed between any two LPIA sequences (see Table 3.1). Finally,

our analysis of ecological guilds in the pre-LPIA and LPIA sequences indicates that guild composition, total guild diversity (Fig. 3.9), and within guild diversity (Fig. 3.10) remained mostly constant from the pre-LPIA interval to the LPIA interval, although the abundance of particular guilds did fluctuate (Fig. 3.11). Together, these results suggest that unlike global diversity, regional taxonomic and guild diversity persisted largely unchanged across the onset of the LPIA. Furthermore, our results indicate that the major transition from the pre-LPIA to the LPIA interval produced changes to the regional biota that were no greater in magnitude than those observed between the seemingly more minor fluctuations between depositional sequences in the LPIA interval.

Potential Biases

In an earlier section, we argued that differences in the sampling of the pre-LPIA and LPIA intervals would not bias the results of this study because analyses were carried out at the sequence level and all the sequences used in our analyses were represented by a similar number of samples. However, although we collected a comparable number of samples from each sequence we were not able to as evenly sample depositional environments from pre-LPIA and LPIA sequences due to changes in the nature of the carbonate ramp through time (see Fig. 3.3) and in the availability of outcrop exposures. This is especially true of the skeletal bank environment, which was intensely and evenly collected in the LPIA sequences, but poorly sampled in the pre-LPIA (sequence 1). Given this discrepancy, it is fair to ask whether a better sampling of the pre-LPIA skeletal bank environment would have yielded significantly more pre-LPIA taxa and thus increased the overall diversity of the pre-LPIA interval relative to the LPIA interval. If

this were indeed true, then the results that we have presented here would be biased in favor of detecting either no change or an increase in regional taxonomic diversity across the onset of the LPIA, and hinder the ability to detect a regional decrease in diversity similar to the one that has been documented at the global scale (see Stanley and Powell, 2003).

To address this question we searched the literature for taxonomic and paleoecologic descriptions of the fauna from the Ste. Genevieve Fm. (sequences 1-3) from the Illinois Basin. Our search yielded only a single study – an examination of the Ste. Genevieve fauna from Illinois that was conducted by Weller (1916). Data from this study, which were collected from a range of lithologies within the formation, indicate that our collection of Ste. Genevieve brachiopod, bryozoan, and trilobite taxa is nearly complete despite our limited sampling. For example, Weller (1916) recovered only one additional brachiopod genus, *Pugnoides,* than we did. In addition, Weller's lists do not include any new bryozoan or trilobite taxa that we had not already encountered in our own samples. That said, our list of bivalve and gastropod taxa is less complete than Weller's, although bivalves and gastropods were exceedingly rare throughout the entire study interval and so poorly preserved that they could not identified to a taxonomic level below "bivalve or gastropod indeterminate". Given that the Chesterian Series in the study area is dominated by bryozoan and brachiopod taxa and that many pre-LPIA taxa were fairly widespread across habitats on the pre-LPIA carbonate ramp (see Chapter 2), we feel it is unlikely that the pre-LPIA skeletal bank environment would harbor a significant number of unique taxa that neither we, nor Weller (1916), recovered. Therefore, while it is likely that we did not collect every taxon present in the skeletal

bank environment in the study area, our literature-based comparisons certainly suggest that we captured a representative Ste. Genevieve fauna and that, at worst, we are missing only the most rare and poorly preserved taxa from the interval. Thus, we feel reasonably confident that additional sampling of the skeletal bank habitat in the Ste. Genevieve Fm. would not have yielded a significant number of new taxa.

**Linking Regional Ecologic and Taxonomic Patterns**

In Chapter 2, we argued that faunal differentiation decreased among biofacies and habitats within the Illinois Basin during the LPIA interval. We suggested that this regional ecological change was consistent with a documented global increase in eurytopy following the onset of the LPIA that has been attributed to the elimination of taxa with narrow geographic ranges (see Powell 2005). The results of the current study, however, fail to detect a significant regional extinction event and indicate that regional (per-sequence) diversity patterns do not match the trajectory of global diversity across the onset of the LPIA. Therefore, at least within the Illinois Basin region, there appears to be a decoupling of biotic gradient and diversity patterns because regional levels of eurytopy increased without evidence for regional extinction of stenotopes (hypotheses for the increase in eurytopy within the Illinois Basin are discussed in Chapter 2). One potentially interesting direction for future research would be to examine geographic variability in the timing, magnitude, and nature of diversity and ecological changes during the LPIA interval in other basins around the globe. This would allow us to examine how pervasive our regional ecologic and diversity patterns are during this interval. As a first step, we examine geographic variability in the response of Chesterian

faunas to environmental changes that occurred during the LPIA in Chapter 4, using correlative LPIA sequences from the nearby Appalachian Basin.

**Comparison with Other studies**

Multiple studies have shown that global rates of origination and/or extinction decreased greatly during the Middle Carboniferous (Raup and Sepkoski 1982, Sepkoski 1998, Stanley and Powell 2003, Stanley 2007), around the time of the late Paleozoic ice age. Likewise, Olszewski and Patzkowsky (2001a) provisionally suggested that the magnitude and frequency of regional turnover episodes also decreased during the late Paleozoic, paralleling the global decrease in extinction rates (see also DiMichele et al. 2004). Although we did not explicitly calculate rates of turnover through the Chesterian, our results are consistent with the notion that regional turnover was relatively lower during the late Paleozoic than it was during the early Paleozoic (Raup and Sepkoski 1982, Sepkoski 1998, Olszewski and Patzkowsky 2001a, Stanley and Powell 2003, DiMichele et al. 2004, Stanley 2007). For example, in a study of early Paleozoic trilobite faunas from North America, Westrop (1996) found that high species level turnover was the norm throughout a 5 Myr duration of the Upper Cambrian Sunwaptan Stage and that genus level persistence was interrupted by trilobite mass extinction events. In addition, Westrop (1996) also noted that the richness of trilobite biofacies was highly variable through 0.1-1.0 Myr cycles in the study interval. Likewise, in their study of Middle and Upper Ordovician brachiopod assemblages, Patzkowsky and Holland (1997) detected significant species and generic level turnover throughout an approximately 17 Myr study interval that spanned 13 depositional sequences (average duration 1.3 Myr) and three

ecological evolutionary subunits (EE subunits) in North America. These authors found characteristically high levels of species turnover within EE subunits (< 10% species persistence) and between EE subunits (10% or less species carryover and holdover).

In contrast, research on middle to late Paleozoic faunas suggests that relatively lower levels of turnover are common. Brett and Baird (1995) reported that brachiopod-dominated Middle Devonian assemblages from the Appalachian Basin of eastern North America displayed high levels of species and generic persistence (60%-80% species carryover and holdover) and relatively unchanging species diversity within EE subunits that lasted up to 8 Myr. Similarly, Bennington and Bambach (1996) also noted that species and generic level turnover was low within Middle Pennsylvanian brachiopod assemblages from the Appalachian Basin, despite finding significant variability in the abundance structures of the assemblages they examined. Data from J B. Bennington's dissertation (see Table D1 from Bennington 1995) indicate that low levels of turnover were common throughout the nearly 10 Myr study interval, which was characterized by 75% to 81% species carryover, 55% to 78. 9% species holdover, and intermediate to low Jaccard Coefficient turnover values ($S_j$ = 0.46 to 0.63) from one marine unit to the next. Olszewski and Patzkowsky (2001a) reported that Pennsylvanian and Permian brachiopod and bivalve assemblages underwent only one period each of elevated turnover though a 12.5 Myr interval that spanned the Pennsylvanian/Permian boundary. These authors also showed that Pennsylvanian and Permain taxa had lower per-taxon rates of background turnover (0.22 for species and 0.075 for genera) than the Ordovician taxa studied by Patzkowsky and Holland (1997), which displayed per-taxon rates of turnover ranging from 0.3 to 0.6 for species and 0.1 to 0.4 for genera. Finally, in a study of Upper

Pennsylvanian crinoid biofacies from three cyclothems in the mid-continent region of North America, Holterhoff (1996) found only low levels of compositional turnover between cycles, even though the abundances of genera were highly variable. Using data available from Appendix 2 in Holterhoff (1996), we computed Jaccard Coefficient values ranging between 0.81 and 0.88 between cycles and percent carryover and holdover metrics from 84% to100%. In addition to these marine examples, literature on Paleozoic terrestrial floras also indicates that faunal turnover was relatively uncommon during the late Paleozoic glacial interval (see DiMichele et al. 1996, DiMichele and Phillips 1996, Pfefferkorn et al. 2000, DiMichele et al. 2001, DiMichele et al. 2002, Falcon-Lang 2004).

The findings of our study are consistent with the late Paleozoic research we highlight above. We failed to observe significant changes to regional taxonomic diversity during the 4 Myr Upper Mississippian study interval. We also showed that taxa persisted to a high degree between depositional sequences; for example, 60% to 88% of taxa occurred in consecutive depositional cycles and 76% to 92% of taxa persisted within one recurring habitat during the 2 Myr LPIA interval. Furthermore, our calculated values for faunal turnover between sequences were relatively low ($S_j$ ranges from 0.56 to 0.78), even across the onset of the LPIA, and fell within the ranges that we computed using data from the studies of Brett (1995), Bennington (1995), and Holterhoff (1996).

Given that glacially driven climate and eustatic changes occurred with high frequency during the study interval, one might expect that faunal turnover, not persistence, would be a dominant feature of the fossil record. However, the results from our study suggest that the major transition from greenhouse to icehouse climates and low amplitude to high amplitude glacioeustasy did not strongly influence regional or local

level turnover in the Illinois Basin. Our results are consistent with the findings of quantitative studies of faunal turnover during the late Cenozoic, an interval of similar, frequent climatic oscillations and high amplitude glacioeustasy. For example, multiple studies on Pleistocene reef corals from the Caribbean (Pandolfi 1996, 1999, Pandolfi and Jackson 2001) indicate that the species composition, structure, and diversity of coral associations persisted nearly unchanged through a series of glacials and interglacials and major glacially-driven eustatic cycles. Likewise, Pleistocene reef mollusk assemblages from the Bahamas (Gardiner 2001) and Upper Quaternary benthic mollusk assemblages from Po Plain, Italy (Scarponi and Kowalewski 2004, 2007), also appear to show remarkably low levels of taxonomic turnover through eustatic cycles that spanned 5 Kyr and 125 Kyr, respectively. Given the overall lack of significant faunal change across eustatic cycles in the study interval, and the similar responses of faunas during later intervals of the LPIA, we suggest that faunal persistence, not origination or extinction, was the normal biotic response to glacially induced environmental change during the late Paleozoic icehouse interval.

## Conclusions

The major findings of this study can be summarized as follows:

1. Sample standardized estimates of regional (per sequence) taxonomic diversity in the tropical Illinois Basin remain relatively constant between the pre-LPIA and LPIA intervals, despite well-documented evidence of a decrease in global marine diversity coincident with the onset of the LPIA (see Stanley and Powell, 2003). Additional

field studies are needed, both within and outside of the Carboniferous tropics, to understand whether the patterns we observe in the Illinois Basin are ubiquitous or if there is high degree of geographic variability in the faunal response among basins situated at the same and different latitudes.

2. The transition from the pre-LPIA to the LPIA interval is not associated with high levels of faunal turnover in the Illinois Basin. In fact, we have shown that anywhere from 76.0% to 92.0% of taxa persist from sequence 1 (pre-LPIA) into the sampled LPIA sequences and comprise 63.9% to 75.0% of the collected LPIA taxa. Furthermore, this low level of faunal turnover falls well within the range observed between consecutive LPIA sequences. Thus, the level of turnover associated with the major transition from the pre-LPIA to the LPIA interval in the Illinois Basin appears to be no greater than that between typical sequences during the LPIA interval.
3. Regional (per sequence) diversity and the local diversity of our most evenly sampled environment - the skeletal bank lithofacies - failed to change significantly through most sequences in the LPIA interval, despite evidence for glacially driven climate and eustatic sea-level changes in the region during that time. Likewise, guild diversity and within guild diversity were largely unchanged during the LPIA interval, although the relative abundance of guilds was more variable. Thus, the overall diversity and ecologic structuring of regional ecosystems in the Illinois Basin remained mostly constant through the ~ 2 Myr LPIA study interval.
4. The low levels of turnover that characterize the LPIA interval of the Illinois Basin, parallel well documented global biotic patterns of exceptionally low rates of origination and extinction during the LPIA and of the late Paleozoic in general.

These results are consistent with the findings of other studies that have examined faunal turnover in marine and terrestrial settings during later intervals of the LPIA and suggest that faunal persistence, rather than change, is the norm throughout this interval of high frequency environmental fluctuations.

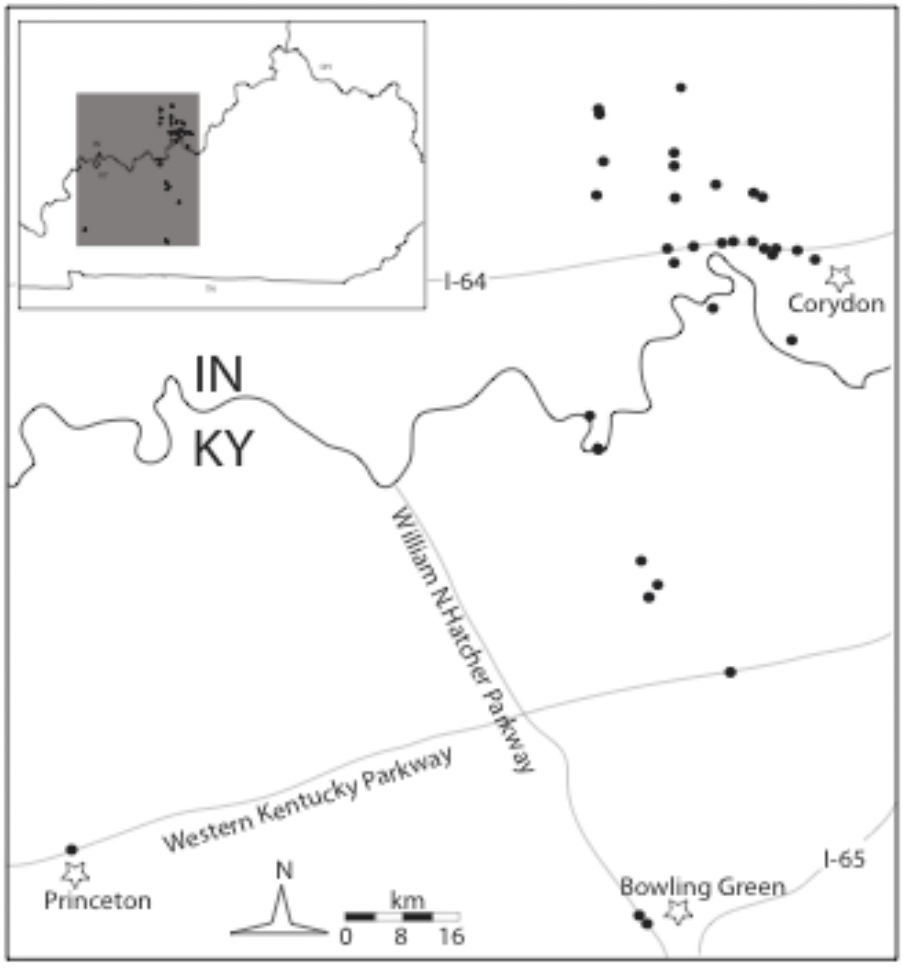



**Figure 3.1. Map of the study area. Black circles represent sampling localities.**

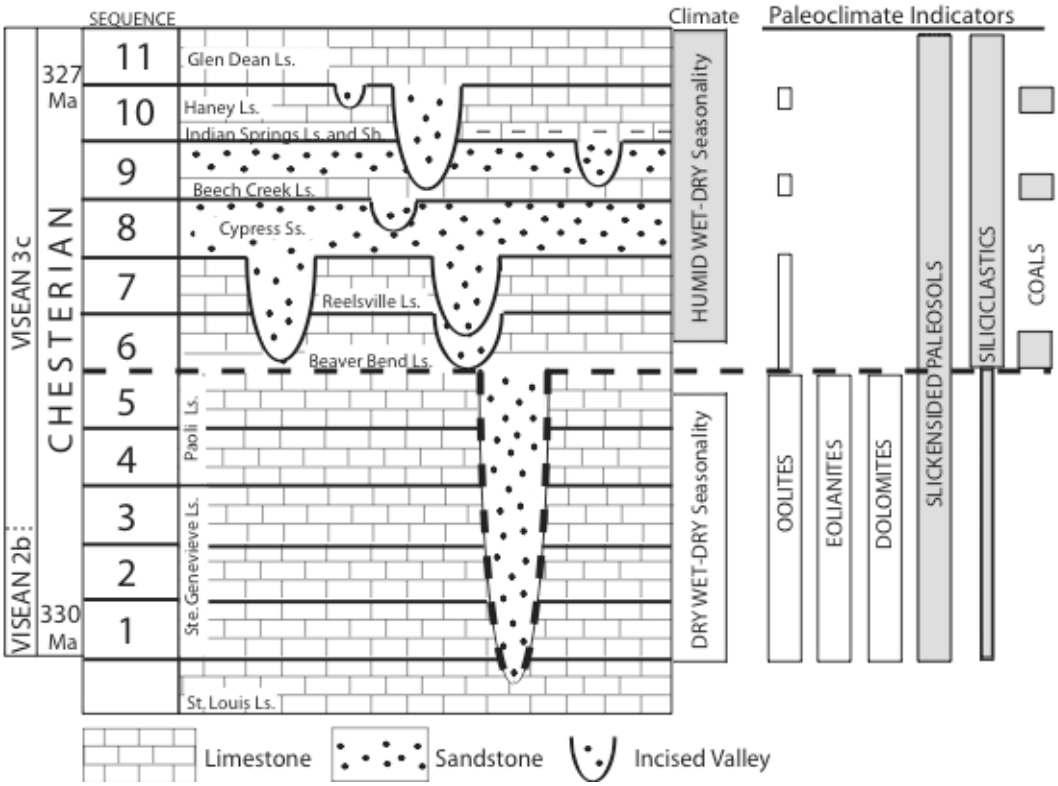
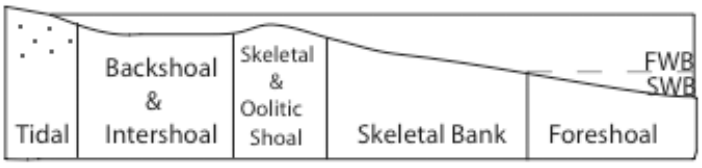


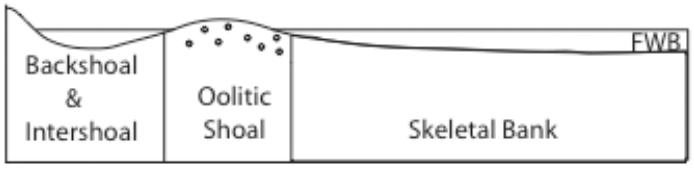

**Figure 3.2. Schematic showing depositional sequences, inferred paleoclimate, and paleoclimatic indicators for the studied interval. Bold dashed line represents the onset of the LPIA.**

A. Sampling of the LPIA Interval




| | Tidal | Backshoal & Intershoal | | Skeletal & Oolitic Shoal | Skeletal Bank | Foreshoal | Number of Samples | Number of Individuals |
|---|---|---|---|---|---|---|---|---|
| **11** | | 8 | | 11 | 14 | | 33 | 3162 |
| **10** | 24 | 4 | | 4 | 10 | 4 | 46 | 2947 |
| **9** | | | | | 14 | 6 | 20 | 1118 |
| **7** | | 6 | | | 15 | 8 | 29 | 2481 |
| **6** | | 3 | *7* | 4 | 17 | | 31 | 1723 |

B. Sampling of the Pre-LPIA Interval




| | Backshoal & Intershoal | | Oolitic Shoal | Skeletal Bank | Number of Samples | Number of Individuals |
|---|---|---|---|---|---|---|
| **5** | 9 | | 4 | | 13 | 164 |
| **1** | 5 | *17* | | 3 | 25 | 1321 |

**Figure 3.3. Time environment plot of number of samples grouped by depositional sequence and environment for: (A) the LPIA interval and (B) the pre-LPIA interval.**

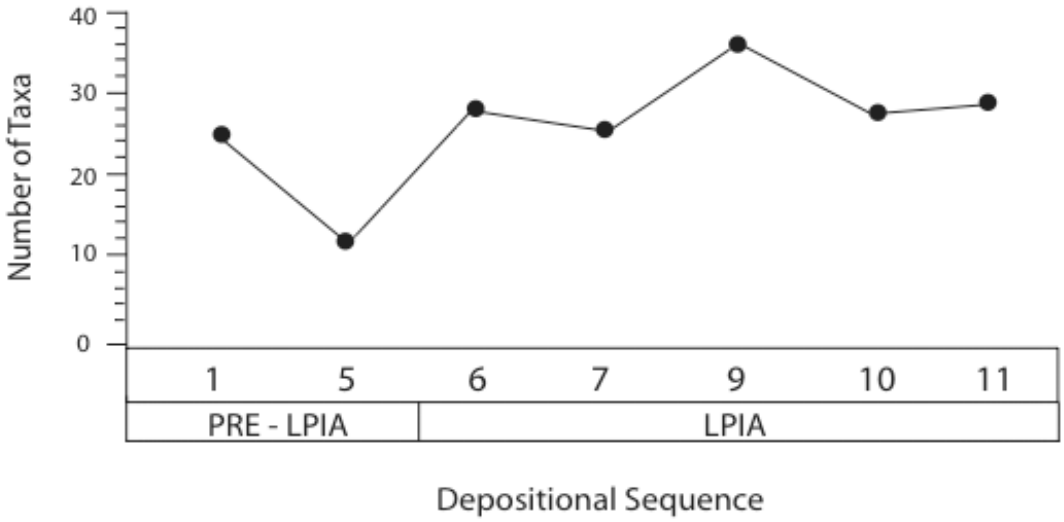



**Figure 3.4. Raw regional (per-sequence) taxonomic diversity. Correlation analysis of taxonomic diversity and the total number of individuals collected for each sequence yields: r=0.46; $r^2$ = 0.21; *p* = 0.29. Correlation analysis of taxonomic diversity and the total number of samples collected for each sequence yields: r = 0.39; $r^2$ = 0.15; *p* = 0.38).**

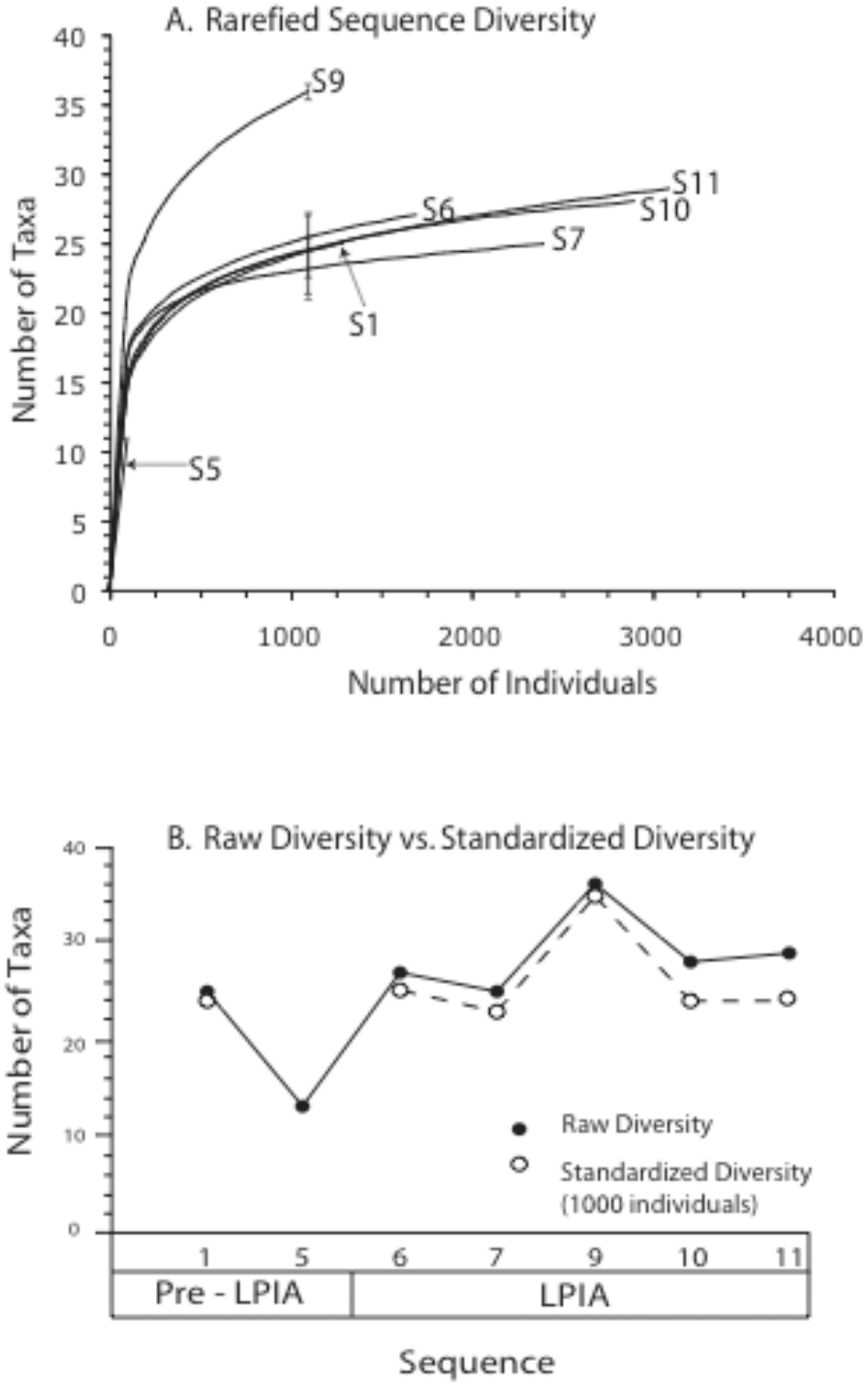



**Figure 3.5. (A) Results from rarefaction analysis of regional (per-sequence) taxonomic diversity. (B) Comparison of raw regional (per-sequence) taxonomic diversity and rarefied regional (per-sequence) taxonomic diversity at a sub-sample size of 1000 individuals. Black circles represent raw diversity; open circles represent rarefied diversity.**

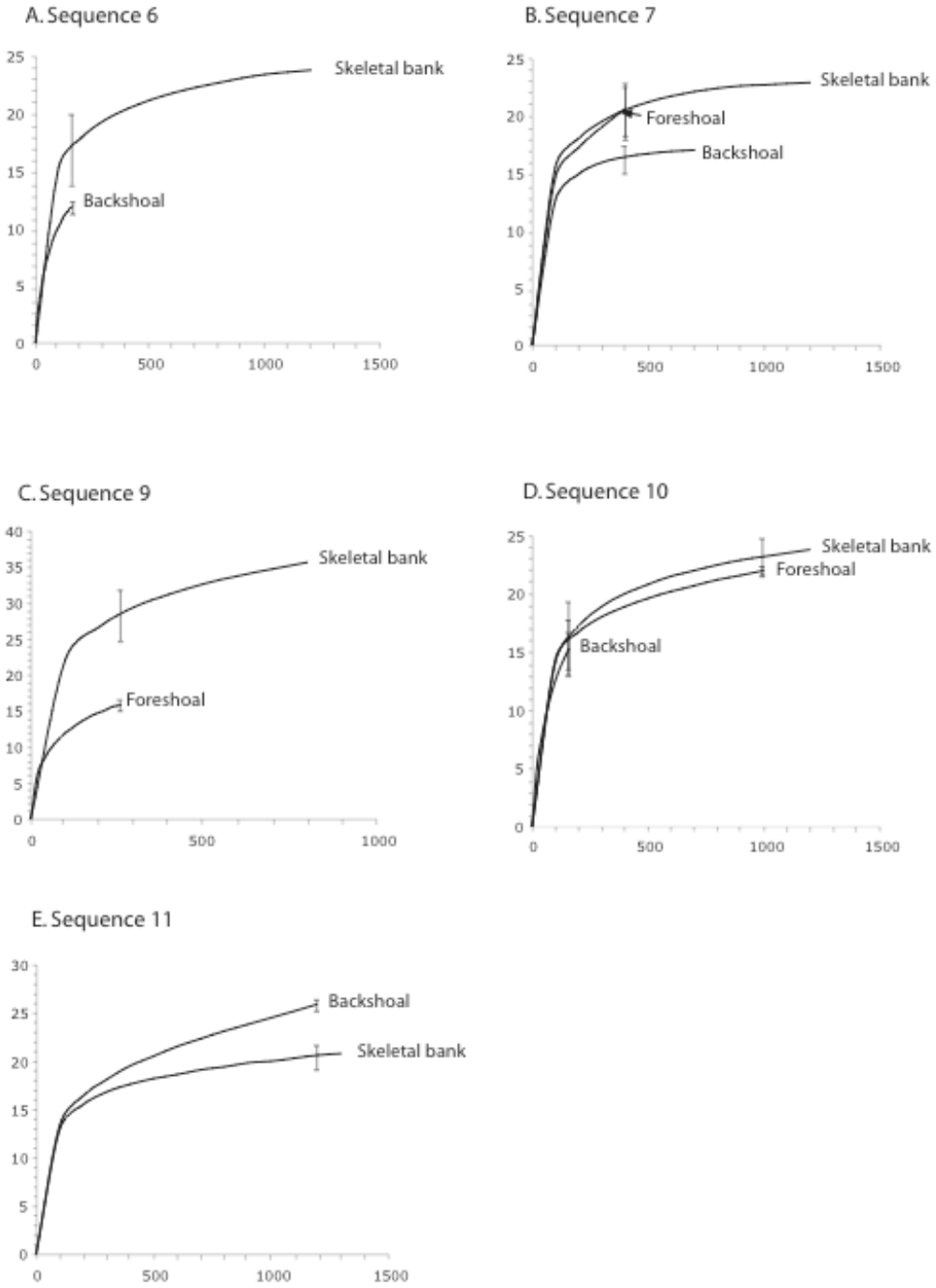



**Figure 3.6. Rarefaction analyses of taxonomic diversity by habitat for: (A) sequence 6, (B) sequence 7, (C) sequence 9, (D) sequence 10, (E) sequence 11.**

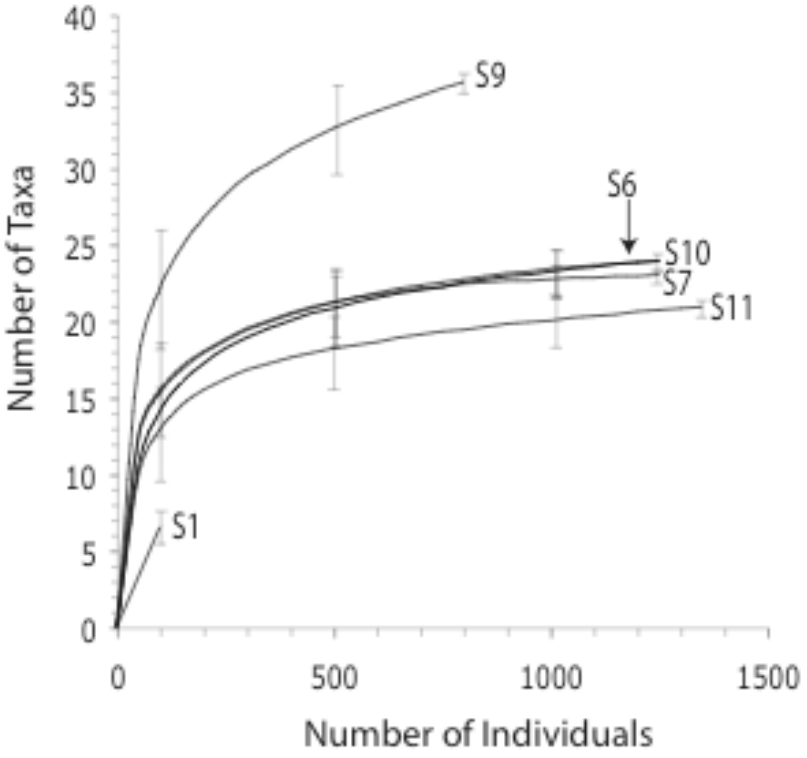



**Figure 3.7. Rarefaction analysis of taxonomic diversity by sequence for the skeletal bank habitat.**

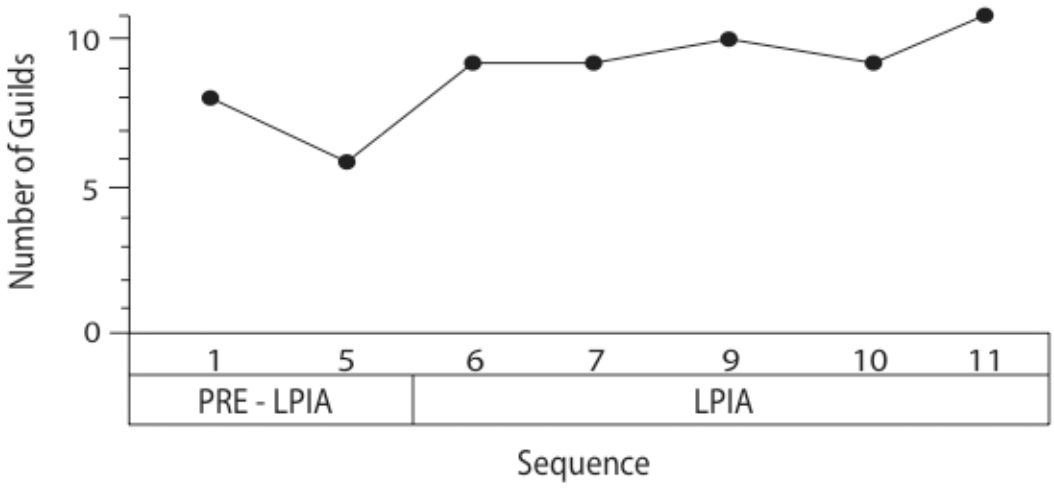



**Figure 3.8. Plot of raw guild diversity by sequence. Guilds are shown in Table 3.4**

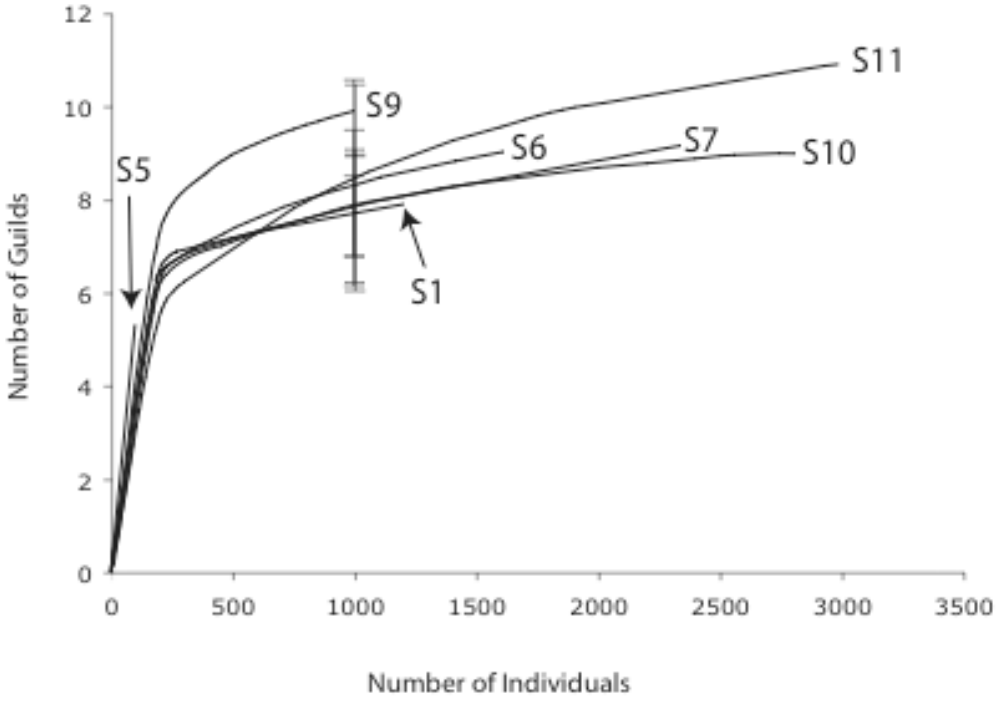



**Figure 3.9. Rarefaction analysis of guild diversity by sequence.**

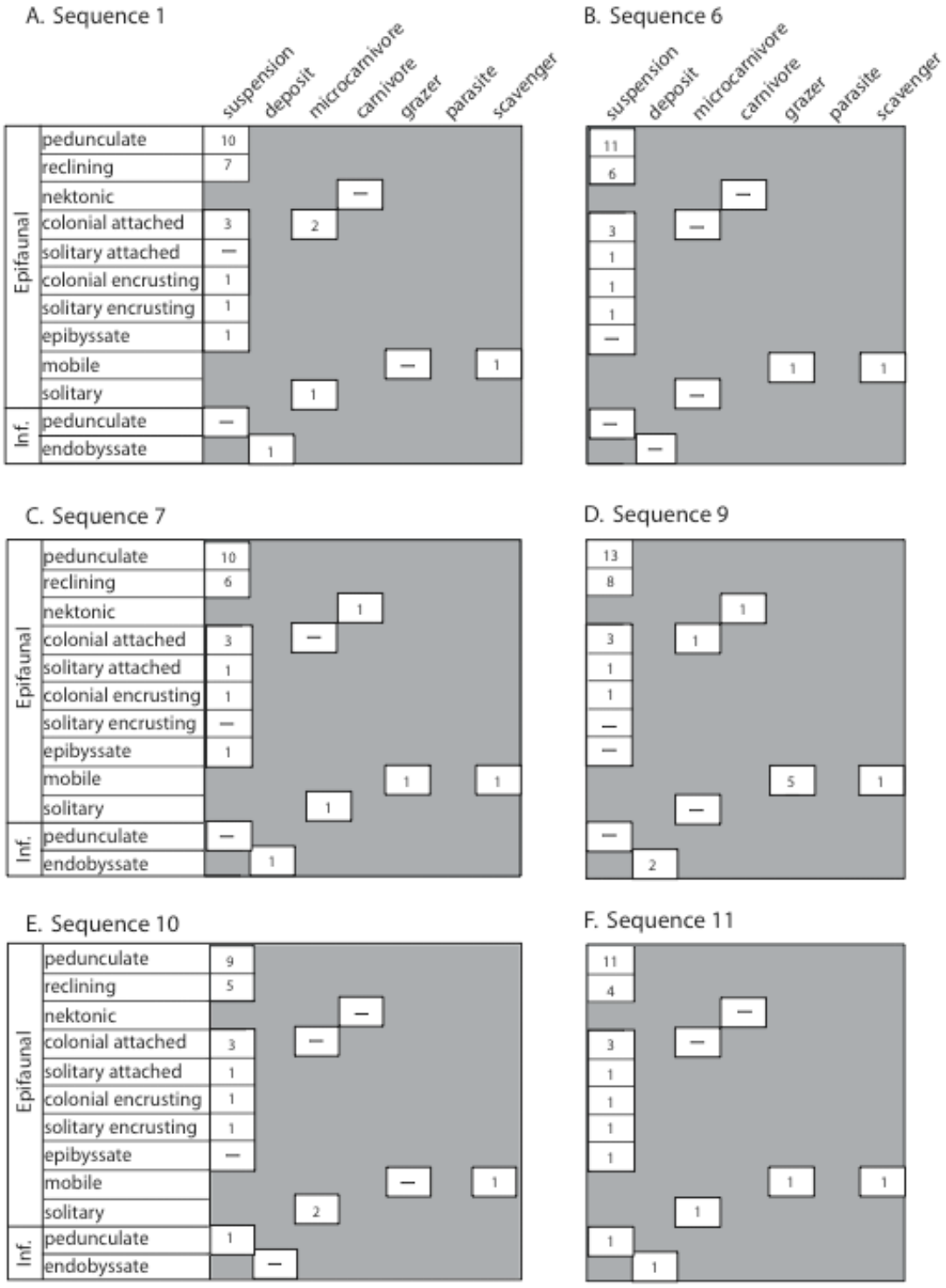



**Figure 3.10. Plots of within guild diversity for: (A) sequence 1, (B) sequence 6, (C) sequence 7, (D) sequence 9, (E) sequence 10, (F) sequence 11.**

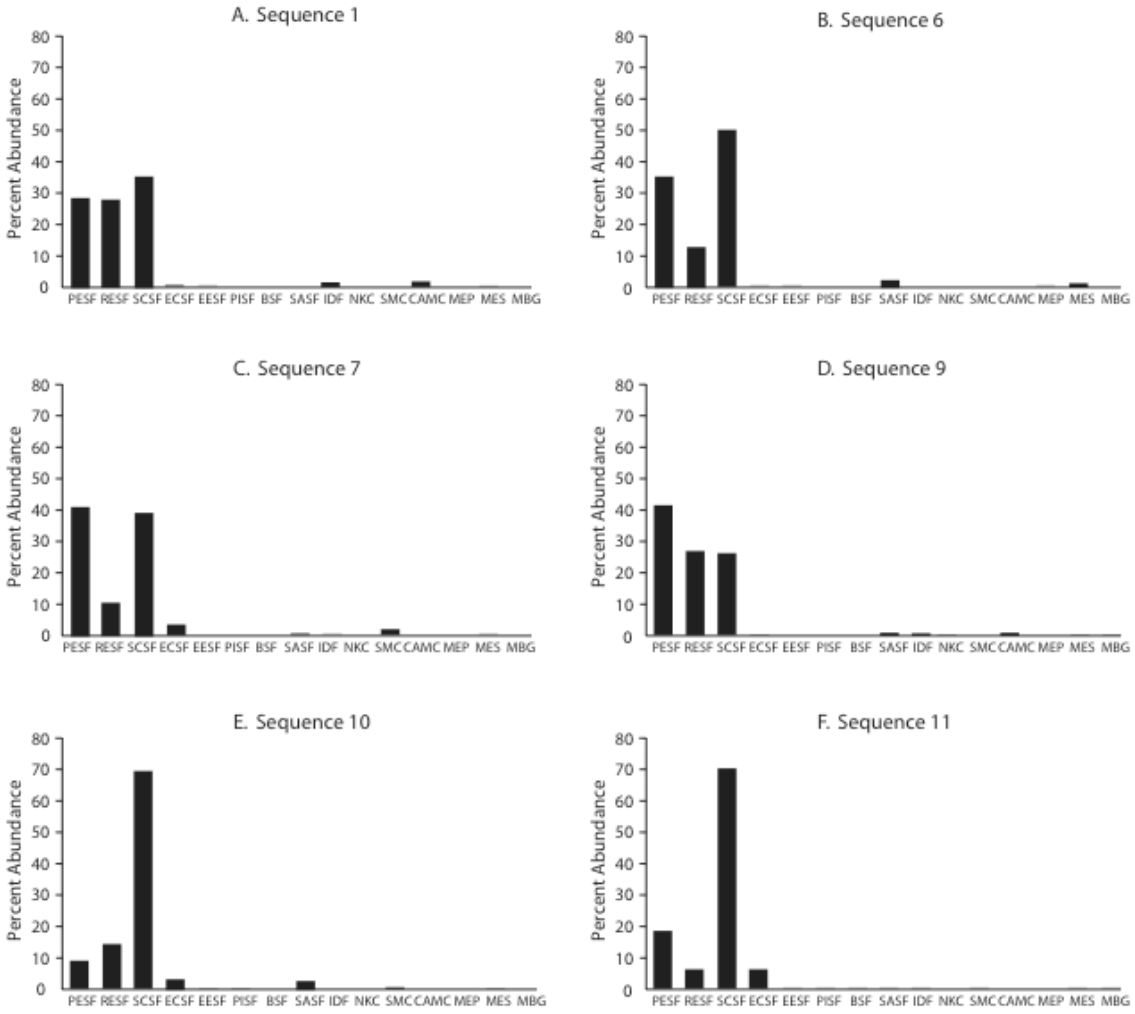



**Figure 3.11. Plots of the relative abundance of guilds for (A) sequence 1, (B) sequence 6, (C) sequence 7, (D) sequence 9, (E) sequence 10, (F) sequence 11. See table 4 for guild abbreviations.**

A.

| Sequences | % Carryover | % Holdover | Turnover (Jaccard Coefficient) |
|---|---|---|---|
| 10 to 11 | 89.2 | 86.2 | 0.78 |
| 9 to 10 | 63.8 | 82.1 | 0.56 |
| 7 to 9 | 88.0 | 61.1 | 0.56 |
| 6 to 7 | 81.5 | 88.0 | 0.73 |
| 5 to 6 | 92.3 | 44.4 | 0.43 |
| 1 to 5 | 48.0 | 92.3 | 0.46 |

B.

| Sequences | % Carryover | % Holdover | Turnover (Jaccard Coefficient) |
|---|---|---|---|
| 1 and 11 | 80.0 | 69.0 | 0.59 |
| 1 and 10 | 84.0 | 75.0 | 0.66 |
| 1 and 9 | 92.0 | 63.9 | 0.61 |
| 1 and 7 | 76.0 | 76.0 | 0.61 |
| 1 and 6 | 80.0 | 74.1 | 0.63 |

**Table 3.1. Percent carryover and holdover metrics and Jaccard Coefficient values obtained from: (A) sequence to sequence comparisons of faunal composition and (B) comparisons of the composition of sequence 1 against each LPIA sequence.**

| Sequences | Turnover (Jaccard Coefficient) Backshoal-Skeletal bank | Turnover (Jaccard Coefficient) Skeletal bank-Foreshoal |
|---|---|---|
| 11 | 0.74 | - |
| 10 | 0.67 | 0.46 |
| 9 | - | 0.44 |
| 7 | 0.74 | 0.73 |
| 6 | 0.44 | - |
| 1 | 0.18 | - |

**Table 3.2. Sequence by sequence turnover values based on the Jaccard Coefficient and percent carryover/holdover metrics.**

| Sequences | % Carryover | % Holdover | Turnover (Jaccard Coefficient) |
|---|---|---|---|
| 10 to 11 | 83.3 | 95.2 | 0.80 |
| 9 to 10 | 55.5 | 83.3 | 0.50 |
| 7 to 9 | 95.6 | 61.1 | 0.60 |
| 6 to 7 | 87.5 | 91.3 | 0.81 |
| 1 to 6 | 85.7 | 25.0 | 0.24 |

**Table 3.3. Per-sequence turnover metrics for the skeletal bank environment.**

| Guild | Code | Taxa |
|---|---|---|
| Colonial microcarnivore | CAMC | *Columnaria, Lithostrotian* |
| Encrusting colonial suspension feeder | ECSF | *fistuliporid bryozoans* |
| Encrusting epifaunal suspension feeder | EESF | *Orbiculoidea* |
| Epibyssate suspension feeder | BSF | *Aviculopecten* |
| Infaunal deposit feeder | IDF | *Edmondia, Nuculopsis, Wilkingia* |
| Mobile epifaunal parasite | MEP | *Platyceras* |
| Mobile epifaunal scavenger | MES | *Paladin* |
| Mobile grazer | MBG | *Euomphalus, Euphemites, Globozyga, Naticopsis,Paleozygolpeura, Strophostylus, Trepospira* |
| Nektonic carnivore | NKC | *Orthoceras, Triptoceroides* |
| Pedunculate epifaunal suspension feeder | PESF | *Anthracospirifer, Athyris, Cleiothyridina, Composita, Dielasma, Eumetria, Girtyella, Martinia, Punctospirifer, Reticulariina, Rhyncopora, Spirifer, Toryinfer* |
| Pedunculate infaunal suspension feeder | PISF | *Lingula* |
| Reclining epifaunal suspension feeder | RESF | *Buxtonia, Chonetes, Dictyoclostus, Echinoconchus, Orthotetes, Ovatia, Productus, Schellwienella, Schuchertella* |
| Sessile colonial suspension feeder | SCSF | *fenestrate, rhabdomesid, and trepostome bryozoans* |
| Solitary attached suspension feeder | SASF | *Pentremites* |
| Solitary microcarnivore | SMC | *Triplophyllites* |

**Table 3.4. List of the guild designations used in this study. Guild abbreviations and the taxa comprising each guild are also shown.**

# Chapter 4. Did the Faunal Response to Environmental Change Vary Geographically During the Late Paleozoic Ice Age? Evidence from the Chesterian Series, Appalachian and Illinois Basins, USA

## Introduction

In recent years, the ability to detect, describe, and interpret biotic and environmental change in the geologic record has increased greatly as earth scientists have begun to integrate the disciplines of sequence stratigraphy and paleoecology. For example, taphonomic data have provided information that is crucial for identifying depositional environments and interpreting key stratigraphic surfaces and depositional cycles that form in response to changes in eustatic sea level, subsidence, and sedimentation rate (see Brett and Baird 1986, Kidwell 1988, 1991a, 1991b, Kidwell and Bosence 1991, Brett and Baird 1993, Brett 1995, 1998). Likewise, sequence stratigraphy has provided information that is essential for evaluating apparent ecological and evolutionary events in the fossil record. Model and field based studies indicate that the distribution of origination and extinction events can be biased heavily by abrupt facies and sedimentation changes associated with changes in sequence architecture (Holland 1995, Holland and Patzkowsky 1999, Holland 2000, Holland and Patzkowsky 2002).

Importantly, sequence stratigraphy also provides a tool for correlating temporally constrained packages of rock bounded by unconformities (depositional sequences) across large geographic areas. Given the recent interest in understanding whether global biotic patterns are meaningful, how they are manifest at regional scales, and how those regional patterns may vary geographically among depositional basins (cf. Jablonski 1998, Miller 1998, Patzkowsky 1999, Miller 2000, Adrain and Westrop 2003, Miller 2003, Sims 2003,

Vermeij and Leighton 2003), this is no trivial matter. Multiple studies have utilized a sequence stratigraphic framework to examine intra-basinal biotic change in relation to global or regional physical perturbation (e.g. Brett and Baird 1995, Bennington 1996, Bennington and Bambach 1996, Patzkowsky and Holland 1997, 1999, Olszewski and Patzkowsky 2001b, 2001a, Bennington 2002, Hendy and Kamp 2004, Holland and Patzkowsky 2004, Scarponi and Kowalewski 2004, Butts 2005, Patzkowsky and Holland 2005, Bonelli et al. 2006, Brett et al. 2007, Hendy and Kamp 2007, Holland and Patzkowsky 2007, Patzkowsky and Holland 2007, Scarponi and Kowalewski 2007). However, no studies have examined quantitatively the degree to which faunal patterns vary between local basins, i.e., within or among depositional sequences that have been correlated between regions. Despite this paucity of work, such an undertaking is crucial for understanding the spatial dynamics of ecological and evolutionary change during intervals of major environmental perturbation and revealing what global patterns can tell us about the patterns and processes acting at the regional and local levels (Vermeij and Leighton 2003).

The Chesterian Series (Upper Mississippian) of the Appalachian and Illinois basins provides an time and place to examine inter-basinal variability in taxonomic diversity, faunal composition, and the structure of biotic gradients during an interval of global biotic and environmental change. Recently, Chesterian strata from the Appalachian and Illinois basins have been placed within a high-resolution sequence stratigraphic framework of fourth-order (~300-450 Kyr) depositional sequences, which have been correlated over 300 km between regions (Smith and Read 1999, Smith et al. 2001b, Smith and Read 2001, Nelson et al. 2002, Al-Tawil and Read 2003, Al-Tawil et

al. 2003). These strata record climate and sea level changes associated with the onset of the late Paleozoic ice age (LPIA), and provide a unique opportunity to compare regional biotic patterns over a broad geographic area and assess inter-regional variability in the response faunas to cyclic eustatic sea level changes.

In this chapter, we provide the first study of its kind to compare geographic and temporal patterns of taxonomic richness, turnover, faunal composition, and ecosystem structure within and between correlative sequences in two separate depositional basins. This study builds upon the results displayed in chapters 2 and 3 by providing an important and comparable dataset against which Illinois Basin faunal patterns can be compared. Importantly, this research also outlines a methodology and research agenda that we believe can be followed to more fully examine regional variability during the LPIA, but that can also be applied to other time intervals throughout the Phanerozoic. Thus, we feel that this study takes a significant first step toward understanding similarities and differences in regional biotic patterns during the LPIA and, in the broader sense, toward assessing the relationship between biotic patterns at the global and regional levels during the LPIA.

## Geologic Background

Strata of the Upper Mississippian Chesterian Series are well exposed across the Appalachian and Illinois basins of the central and eastern United States. The data used in this study come from 23 outcrops located throughout western and eastern Kentucky, southern Indiana, and northern Tennessee (Fig. 4.1; Appendix B). In the study area, the

Chesterian interval is comprised of carbonate and mixed carbonate and siliciclastic sedimentary rocks deposited during the Upper Mississippian (Visean 3b-3c) and encompass approximately 4 Myr based upon the radiometric dating of zircons from correlative strata in Australia (Roberts et al. 1995).

**Appalachian Basin**

Chesterian strata are exposed in a narrow, northeast to southwest trending outcrop belt along the distal margin of the Appalachian Basin in eastern Kentucky (Fig. 4.1). During the Chesterian, the Appalachian Basin was located approximately 25° south of the equator in a semiarid desert belt (De Witt and McGrew 1979, Scotese and McKerrow 1990). The Chesterian Series is comprised of eleven fourth-order depositional sequences, which were deposited during the transition into the late Paleozoic ice age (see Fig. 4.2). Sequences 1-7 (Ste. Genevieve through Paoli formations) consist primarily of carbonate-dominated lithofacies that were deposited as oolitic shoals, lagoonal muds, and lesser skeletal bank sediments in a very shallow, tide and wave-agitated marine setting (Al-Tawil and Read 2003). These sequences were formed under moderate sea level fluctuations that repeatedly flooded the shallow ramp to depths of no more than 10 m (Al-Tawil and Read 2003). Sequences 8-11 (Beaver Bend through Glen Dean formations) are comprised of mixed carbonate and siliciclastic sedimentary rocks that were deposited on a steeper ramp. These sequences contain widespread skeletal grainstones, packstones, and wackestones that were deposited in more stable, open marine environments along middle and outer ramp settings (Fig. 4.3; Al-Tawil and Read 2003). The gradual transition from shallow water carbonate dominated facies of

sequences 1-7 to mixed carbonate and siliciclastic dominated open marine facies in sequences 8-11 reflects, in part, environmental shifts that occurred during the latest Mississippian and coincided with the start of the LPIA; these include: (1) a change from a semi-arid to more humid climates, (2) a shift toward higher amplitude glacio-eustasy (Al-Tawil and Read 2003), and (3) an increase in subsidence due to regional flexure of the Appalachian basin (Al-Tawil and Read 2003).

**Relationship with Chesterian Sequences in the Illinois Basin**

Al-Tawil and coworkers mapped the distribution of carbonate facies, paleosols, key stratigraphic surfaces, and biostratigraphic markers within a sequence stratigraphic framework across the Appalachian Basin, using high-resolution cross sections constructed with detailed stratigraphic logs from outcrops and cores (Al-Tawil and Read 2003, Al-Tawil et al. 2003). Building upon the findings of earlier studies of Chesterian strata in the region (see McFarlan and Walker 1956, Ettensohn and Dever 1979, Dever 1980, Ettensohn 1980b, 1980a), Al-Tawil and coworkers demonstrated that it was possible to trace regional sequences westward into the Illinois Basin, where they were correlative with fourth order depositional sequences that had been established previously (see Smith and Read 1999, Smith and Read 2000, Smith et al. 2001b, Smith and Read 2001, Nelson et al. 2002) .

As in the Appalachian Basin, there are marked changes in the nature of depositional sequences following the start of the LPIA in the Illinois Basin (these are discussed in detail in chapters 2 and 3) and include: 1) an increase in coarse siliciclastic influx; 2) the presence of deeply incised valleys; 3) an increase in the distribution of

moderate and deeper water facies along the ramp; and 4) a decrease in the distribution of shallow water and oolite facies (Smith and Read 1999, 2000, Smith et al. 2001b, Smith and Read 2001). These comparable features suggest that the Illinois and Appalachian Basins were affected in similar ways by the eustatic, climatic, and tectonic changes that occurred during the study interval.

**Boundaries Between Basins**

The Cincinnati Arch, Waverly Arch, Jessamine (Lexington) Dome, and Nashville Dome were topographic highs that were active in the study area during the Chesterian (see Fig. 4.1; Woodward 1961, Pryor and Sable 1974, Ettensohn 1980b, 1980a, Sable and Dever 1990, Dever 1999). These four structures formed the western margin of Appalachian Basin, separating it from the Illinois Basin. Despite these, the Appalachian and Illinois Basins remained connected throughout the study interval by way of the Cumberland Saddle, a topographic low situated along the trend of the Cincinnati Arch, which provided an open passageway between regions (Al-Tawil and Read 2003).

**Study Interval**

We focus our study on two of the eleven depositional sequences in the study area: sequence 10, which is comprised of the Haney Formation, and sequence 11, which consists of the Glen Dean Formation (Fig. 4.2). These sequences were chosen because they are widely exposed across the Appalachian and Illinois basins and contain lithofacies and faunas that have been well described in the literature (Coryell and Rozanski 1942, Haas 1946, Horowitz 1956, Perry and Utgaard 1960, Rodriguez 1960,

Perry and Horowitz 1963, Horowitz 1965, Vincent 1975, Ettensohn and Dever 1979, Dever 1980, Ettensohn 1980b, 1980a, Kelly 1984, Chestnut and Ettensohn 1988, Treworgy 1988, Horowitz 1992, Smith and Read 2001, Nelson et al. 2002, Al-Tawil and Read 2003, Al-Tawil et al. 2003). The Haney and Glen Dean sequences are comprised of five fossiliferous marine lithofacies; tidal sand, backshoal, skeletal/oolitic shoal, skeletal bank, and the foreshoal (see Fig. 4.3). The tidal flat facies consists of orange to grey, very fine-medium grained, cross to massive bedded, quartz sandstone that formed in a tide dominated, shallow marine environment (Huff 1993, Smith and Read 1999, 2001, Nelson et al. 2002). The backshoal facies is dominantly fissile, olive green to black fossiliferous shale that may be interbedded with wackestone and packstone; it represents deposition in protected, shallow water, low energy settings behind skeletal/oolitic shoals (Smith and Read 2001, Al-Tawil and Read 2003). The skeletal/oolitic shoal facies is comprised of grey to white, cross-bedded, oolitic, skeletal grainstones that formed in a high energy environment (Smith and Read 2001, Al-Tawil and Read 2003). The skeletal bank habitat formed in a high to moderate energy environment on the inner to middle ramp. It is comprised of grey, thin to thick bedded, massive to cross-bedded, skeletal grainstones and packstones (Smith and Read 2001, Al-Tawil and Read 2003). The foreshoal environment consists of medium to dark grey, thick to massive bedded, skeletal wackestone and mudstones that were deposited above storm wave base; the foreshoal represents the most distal environmental sampled along the carbonate ramp (see Fig. 4.3).

## Faunal Data

The raw dataset for this study consists of 10,045 specimens from 153 samples (Fig. 4.4). At each sampling locality we collected two to five laterally distributed bulk samples from fossiliferous lithofacies to reduce the effects of spatial patchiness on estimates of fossil diversity or abundance (cf Bennington and Rutherford 1999, Bennington 2003). All samples were returned to the lab where they were washed with detergent, manually disaggregated, and examined using a binocular microscope. Every fossil specimen was identified to the finest taxonomic level possible using the *Treatise on Invertebrate Paleontology* and literature on Chesterian taxonomy (e.g., Weller 1916, Weller 1931, 1936, Sutton 1938a, McFarlan 1942, Moore 1948, Brookley 1955, Horowitz 1956, Rodriguez 1960, Perry and Horowitz 1963, Horowitz 1965, Thein and Nitecki 1974, Brezinski 1988, Chestnut and Ettensohn 1988, Busanus and Hoare 1991, Henry and Gordon 1992, Hoare 1993). To maximize the use of as much data as possible, all of our analyses have been conducted at the generic level because most specimens, other than bryozoans, could be identified to the genus. Like chapters 2 and 3, bryozoans were identified to the family level. Fossil individuals were counted using the minimum number of individuals (MNI) method, which provides a relatively conservative estimate of fossil abundances (Gilinsky and Bennington 1994). The abundance of colonial organisms, such as bryozoans and corals, was determined by counting each 1 cm length of colony as an individual (see also Patzkowsky and Holland 1999, Holland and Patzkowsky 2004); although there is no clear way to equate the abundance of one colonial taxon with one bivalved taxon (e.g., brachiopod), we feel that this method at

least allowed us to assess the importance of colonial taxa within our data set. In all, 39 taxa were recovered from our samples, which had a mean size of 65.6 individuals (median=42.0).

## Quantitative Methods

### Tabulating Taxonomic Diversity

Analytic rarefaction (Hurlbert 1971, Simberloff 1972, Heck et al. 1975, Raup 1975, Tipper 1979) was used to estimate and compare mean taxonomic diversity at a standardized sample size within and between sequences in the Appalachian Basin and to compare diversity between basins. Rarefaction was performed using the software Analytic Rarefaction v. 1.3, available at Steve Holland's website (www.uga.edu/strata/software/index.html). Statistical differences between the mean diversities calculated from rarefaction were assessed using ninety five percent confidence intervals.

### Tabulating Compositional Turnover

Simple percent carryover/holdover metrics (see Brett and Baird 1995) and the Jaccard Coefficient ($S_j$) (Jaccard 1908) were used to quantify faunal turnover within and between sequences in each basin. In this study percent carryover metrics quantify the total percentage of taxa that persist from the Haney sequence into the Glen Dean sequence, or from the Appalachian Basin into the Illinois Basin. The percent holdover metric quantifies the percentage of the fauna from the Glen Dean sequence that is

comprised of taxa that "carryover" from the Haney sequence, or the percentage of Illinois Basin fauna that is comprised of taxa from the Appalachian Basin.

The Jaccard Coefficient measures the proportion of taxa shared between two sequences or basins using the following formula:

$$S_j = \frac{T_C}{T_1 + T_2 - T_C}$$

where $T_1$ is the number of taxa in a sequence or basin, $T_2$ is the number of taxa in the other sequence or basin sample 2, and $T_C$ is the number of taxa shared between the two sequences or basins. The Jaccard Coefficient ranges from 0 to 1 and provides an inverse measurement of taxonomic turnover, i.e., smaller Jaccard values indicate greater faunal turnover between sequences or basins.

**Examining Biotic Gradients**

To be methodologically consistent with chapters 2 and 3, we used a combination of multivariate and non-parametric techniques to examine biotic gradients in the Haney and Glen Dean sequences of the Appalachian Basin. Q and R-mode cluster analyses were used to define biofacies using the CLUSTER package for R (R Project 2007). In order to emphasize the contributions of all taxa, rather than only the most abundant, we performed a log transformation on sample counts prior to clustering (McCune and Grace 2002). Cluster analyses were performed with agglomerative nesting, Euclidean distance, and Ward's linkage method, which fuses samples to existing clusters by minimizing the error sum of squares (see McCune and Grace 2002).

Detrended correspondence analysis, or DCA (Hill and Gauch 1980), was utilized to explore underlying environmental gradients in each sequence. DCA simultaneously ordinates samples and taxa along axes in ordination space that are determined analytically to capture primary vectors of variability in the data (McCune and Grace 2002). DCA was performed using DECORANA from the VEGAN package in R (R Project 2007).

Analysis of Similarities (ANOSIM) was applied to examine differences in the structure of biotic assemblages between basins (within a sequence) and through time (among sequences). ANOSIM is a non-parametric technique that uses the rank order of Bray Curtis dissimilarity values to test statistically for differences among sample groupings that have been defined *a priori* (Clarke 1993). The ANOSIM test statistic, *R*, provides an absolute measure of compositional differences among the groups being evaluated, on a scale that typically ranges from 0 (the ranks of similarities within and among groups are the same; i.e., the groups are indistinguishable) to 1 (the ranks of sample similarities within groups are more similar to each other than those between groups; i.e., the groups are different). In order to interpret the meaning of ANOSIM *R* values falling between 0 and 1, Clarke and Gorely (2001) have provided the following guideline: with $R > 0.75$, groups are distinct; with $R > 0.5$, groups are overlapping, but clearly different; with $R > 0.25$, groups overlap strongly; and with $R < 0.25$, groups are barely distinguishable. ANOSIM was performed using the ANOSIM function from the VEGAN package in R (R Project 2007).

# RESULTS

## Haney Sequence: The Structure and Composition of Biotic Gradients

### Biofacies Description

Seven biofacies are recognized in the Haney sequence of the Appalachian Basin (Fig. 4.5, right): (1) *Anthracospirifer-Martinia-Composita*, (2) *Martinia-Orthotetes*, (3) trepostome-*Anthracospirifer*-fenestrate-rhabdomesid-*Eumetria-Composita*, (4) *Anthracospirifer*-fenestrate-*Productus -Cleiothyridina*, (5) fenestrate-rhabdomesid-*Reticulariina-Orthotetes*, (6) *Productus-Anthracospirifer-Composita*, and (7) *Productus*. *Anthracospirifer* is a common component in four of these biofacies, but is especially dominant in biofacies 1 and 4. Fenestrate bryozoans are common to biofacies 3 and 4, but are most important in biofacies 5 where they account for 58% of individuals. Trepostome bryozoans occur in abundance only in biofacies 3 (27%), but rhabdomesid bryozoans are encountered commonly in biofacies 3 and 5. The productid brachiopod, *Productus*, is common to biofacies 4, although it attains its greatest abundances in biofacies 6 and 7 (49.8% and 94.7% respectively). *Martinia* is the most abundant taxon in biofacies 2 (78%), but is far less important in biofacies 1 where it accounts for 12.5% of individuals. The brachiopods *Eumetria, Reticulariina, Composita, Cleiothyridina*, and *Orthotetes* are each common to one or two biofacies, but fail to attain very high abundances when present.

Biofacies Relationships

There is very little overlap among samples from different biofacies in ordination space (Fig. 4.5, top). Fenestrate bryozoan dominated samples from biofacies 5 tend to occupy the most negative values along axis 1 and largely segregate from samples of the other biofacies. Samples from biofacies 2-4 occupy low axis 1 values, but are clearly differentiated along axis 2; for example, biofacies 3 tends towards low axis 2 values, while biofacies 4 and 2 occupy intermediate and high scores, respectively. The two *Anthracospirifer* dominated samples of biofacies 1 plot at intermediate to high axis 1 scores where they mix with samples from biofacies 2 and 6. *Productus* dominated samples of biofacies 6 and 7 occupy the most positive axis 1 scores. Depositional environments overlap to a much greater degree than biofacies along DCA axes (Fig. 4.5, middle). The fenestrate bryozoan and brachiopod dominated samples from the tidal and skeletal bank habitats tend to overlap each other along low and intermediate axis 1 scores. Samples from the foreshoal habitat, which are dominated largely by *Anthracospirifer* and *Productus*, are spread across intermediate and positive axis 1 scores, where they overlap with a number of samples from the skeletal bank environment. Axis 1 appears to correspond roughly with water depth, or position along the ramp, as the shallow water, inner ramp tidal environment plots at negative values and moderate and deeper water depth environments of the middle and outer shelf (the skeletal bank and foreshoal) tend to more positive axis 1 values.

Taxa tend to sort along axis 1 following habitat preferences that we inferred previously in Chapter 2 (Fig. 4.5, bottom). The inner to middle ramp environments of the

tidal sand and skeletal bank are comprised of a suite of bryozoan and brachiopod taxa including the fenestrates, rhabdomesids and trepostomes, *Punctospirifer*, and *Reticulariina*. These taxa occupy low to intermediate axis 1 scores. The deep water, low energy, and soft substrate environment of the foreshoal, on the other hand, is dominated by *Productus*, *Anthracospirifer*, *Martinia*, and *Orthotetes*.

**Haney Sequence: Geographic Variability in Biotic Gradients**

The overall structure of the biotic gradient recovered from the Haney sequence in the Appalachian Basin is very similar, although not identical, to that we observed previously from the Haney sequence in the Illinois Basin (described in Chapter 2). For example, within the Illinois Basin, depositional environments also sorted along a primary gradient of water depth during the Haney sequence: inner to middle ramp Haney habitats occurred at low and intermediate DCA axis 1 scores, and outer ramp habitats tended to high axis 1 scores (see Fig. 2.6F, Chapter 2). Moreover, taxa also tended to occupy similar positions along DCA axis 1 in relation to depositional environments: fenestrate, rhabdomesid, and trepostome bryozoans, as well as the brachiopods *Reticulariina* and *Punctospirifer* tended to occupy low axis 1 scores and inhabit inner ramp environments, while *Productus*, *Anthracospirifer*, *Martinia*, and *Orthotetes* tended toward high axis 1 scores and the outer ramp (see Fig. 2.7F, Chapter 2).

However, regional differences exist between Appalachian and Illinois basin Haney biotic gradients as well. One such difference includes major changes in the abundance of dominant taxa between basins. This is illustrated in Table 4.1, which shows lists of the taxa comprising up to 90% of the individuals collected from the Haney

Formation in each basin. Note that *Anthracospirifer* is the most abundant Haney taxon in the Appalachian Basin (22.3%), but accounts for less than 1% of the total individuals sampled from Haney biofacies in the Illinois Basin. Likewise, the importance of fenestrate bryozoans in Haney biofacies also changes. Fenestrate bryozoans comprise approximately 57% of the individuals in Haney biofacies in the Illinois Basin, but only 14% of the individuals in the Appalachian Basin. Despite these interregional changes in the abundances of the most common Haney taxa in both regions, ANOSIM tests indicate a great deal of overlap between Appalachian and Illinois basin Haney faunas in general ($R = 0.36$; $p = <0.001$).

**Haney Sequence: Taxonomic Diversity and Faunal Composition**

The overall taxonomic diversity (richness) and composition of Haney faunas does not vary greatly between the Appalachian and Illinois basins. Rarefaction estimates of mean sequence diversity indicate that at a sample size of 2000 individuals, the Haney sequence was comprised of nearly 25 taxa in each basin (Fig. 4.6). Furthermore, 95% confidence intervals suggest that regional diversity estimates are statistically indistinguishable. Percent carryover/holdover and Jaccard Coefficient turnover metrics imply only a low level of turnover between the two basins (see Table 4.2). Percent carryover values show that nearly 89% of all taxa that were sampled from the Haney sequence in the Appalachian Basin were also recovered in the Illinois Basin. In addition, over 85% of Illinois Basin Haney taxa were comprised of “holdovers” from the Appalachian Basin. Only three Appalachian Basin genera were not sampled in the Illinois Basin, these include: the bivalve *Limipecten* and the brachiopods *Athyris* and

*Schellwienella*. We should note however, that these three genera were exceedingly rare overall and accounted for less than 0.1 % of all individuals recovered from the Haney interval. The Jaccard Coefficient values support the results from percent carryover/holdover metrics and also imply a low level of compositional turnover between basins ($S_j = 0.77$).

Given the overall high level of faunal similarity between basins, we feel it is unlikely that our results are biased by differences in the sampling of environments between regions. However, we performed additional analyses on a restricted subset of our data from the skeletal bank habitat of both regions, because it was our most consistently sampled Haney environment (see Fig. 4.4). The results from the analyses of the skeletal bank fauna are consistent with those from analyses of the whole Haney fauna: an overall moderate to high level of faunal similarity exists between the two basins ($S_j$ = 0.63; ANOSIM $R$ = 0.38; $p$=<0.001). For example, percent carryover metrics indicate that 85% of Appalachian basin skeletal bank taxa were also recorded in the Illinois Basin (Table 4.2). These “carryover” taxa accounted for about 70% of the taxa comprising the skeletal bank fauna of the Illinois Basin (see Table 4.2); only seven taxa were not recorded in both basins, but these taxa were extremely rare in the skeletal bank habitat overall and comprised only <1% to 3% of the individuals collected from the facies. Based on the results from this, and the preceding analyses, we feel confident that there is a high level faunal similarity within the Haney Formation of the Appalachian and Illinois basins.

**Glen Dean Sequence: The Structure and Composition of Biotic Gradients**

Biofacies Description

Five biofacies are identified in the Glen Dean Formation (Fig. 4.7, right): (1) *Anthracospirifer*, (2) *Orthotetes*-trepostome-*Anthracospirifer*-fenestrate-*Composita*, (3) fenestrate-rhabdomesid-fistuliporid, (4) fenestrate-trepostome-*Reticulariina*, and (5) fenestrate. Fenestrate bryozoan taxa are present in moderate and high abundances in most biofacies, especially in biofacies 5 (88.9%). Trepostome bryozoans are abundant in biofacies 2 (25.7%) and common in biofacies 4 (13.4%). Rhabdomesid and fistuliporid bryozoan taxa are common in biofacies 3 (13.6% and 5.4%, respectively), but rare or absent in the remaining biofacies. *Anthracospirifer* is dominant in biofacies 1 (76.7%), but less abundant in biofacies 2 (11.7%) where it appears with *Orthotetes*, *Composita*, and bryozoan taxa. *Reticulariina* is common in biofacies 4 (5.6%).

Biofacies Relationships

DCA results indicate that biofacies are clearly segregated in ordination space (Fig. 4.7, top). Fenestrate bryozoan dominated samples from biofacies 3, 4, and 5, all tend toward negative axis 1 values, but are clearly distinguished along axis 2. For example, biofacies 5 occupies the most negative axis 2 scores, biofacies 4 occupies low negative scores, and biofacies 3 tends towards intermediate and positive values. Samples from biofacies 2 plot at intermediate and low positive axis 1 values and are separated from the *Anthracospirifer* dominated samples of biofacies 1, which occupy the most positive axis 1 values. Glen Dean depositional environments also sort cleanly in ordination space (Fig. 4.7, middle). Samples from the backshoal, skeletal bank and silty skeletal bank, all

occupy negative axis 1 values, but separate along axis 2 with the backshoal at the most negative axis 2 scores, the skeletal bank at low negative scores, and the silty skeletal bank at intermediate and positive values. Samples from the foreshoal habitat plot at intermediate and positive values along axis 1. Much like the Haney Formation, samples from the Glen Dean Formation appear to sort along a water depth or ramp position gradient with inner and middle ramp habitats tending toward negative axis 1 scores and samples from the outer ramp occupying more positive values.

Taxa tend to sort along axis 1 following the environmental tolerances that we inferred previously in our discussion of the Haney fauna (Fig. 4.7, bottom). Bryozoan dominated assemblages tend toward negative axis 1 scores and are most abundant in inner to middle ramp environments like the backshoal and skeletal bank. *Anthracospirifer*, *Martinia*, *Orthotetes*, *Productus*, *Composita*, and *Cleiothyridina* tend toward positive axis 1 scores and are most dominant in the foreshoal habitat of the outer ramp.

**Glen Dean Fauna: Geographic Variability in Biotic Gradients**

Glen Dean faunas of the Appalachian and Illinois basins also display congruent biotic gradients, despite being separated by over 300 km. For example, both regions are comprised of comparable sets of fenestrate bryozoan dominated biofacies (compare Fig. 4.7, right with sequence 11 biofacies in APPENDIX A). Moreover, DCA analyses suggest that these biofacies sort along similar environmental gradients corresponding to water depth, or position along the ramp: shallower habitats occupy negative axis 1 scores and deeper water habitats tend toward positive scores (compare Fig. 4.7, middle with Fig.

2.6G). In addition, taxa also tended to comparable DCA 1 axis scores in ordinations of data from both regions: fenestrate bryozoans, *Pentremites* blastoids, and *Ovatia* tend to inhabit inner ramp habitats and occupy negative DCA axis 1 scores, while *Martinia*, *Orthotetes*, and *Girtyella* occupy middle to outer ramp habitats and tend to positive axis 1 scores (compare Fig. 4.7, bottom with Fig. 2.7G). Finally, unlike the faunas from the Haney sequence, there is a very high degree of overlap among lists of the most abundant Glen Dean taxa from each basin (see Table 4.3). Fenestrate bryozoans appear as the dominant taxon and occur in similar percent abundances in the Appalachian and Illinois basins (55% and 59%, respectively). Likewise, rhabdomesid and trepostome bryozoans, and Eumetria also occur in very similar ranks and abundances across regions. Given the faunal overlap cited above, it is not surprising that results from ANOSIM tests indicate that regional Glen Dean faunas are nearly indistinguishable ($R$=0.14; $p$=<0.001).

**Glen Dean Fauna: Taxonomic Diversity and Faunal Composition**

The overall level of taxonomic richness and faunal composition of Glen Dean faunas from the Appalachian and Illinois basins are similar, but not identical. For example, rarefaction analyses suggest that regional mean diversity was significantly higher within the Illinois basin (26.9 taxa) than it was in the Appalachian Basin (23 taxa), at a sampling intensity of 1900 individuals (Fig. 4.8). Despite this, turnover metrics indicate that faunal turnover was very low between basins during the Glen Dean sequence (see Table 4.2). One hundred percent of the Glen Dean taxa sampled from the Appalachian Basin carried over into the Glen Dean sequence of the Illinois Basin (Table 4.2). Furthermore, these taxa account for approximately 80% of the Illinois Basin Glen

Dean biota (Table 4.2). The remaining 20% (7 taxa) of the Illinois Basin Glen Dean fauna is comprised of very rare taxa that together accounted for only 15 individuals and < 0.5% of the total individuals collected from the Glen Dean sequence. The Jaccard Coefficient turnover metric supports the percent carryover/holdover results and suggests that that the overall compositions of regional Glen Dean faunas overlapped greatly ($S_j$ = 0.79), despite differences in the presence of rare taxa.

Our interpretations do not change when we restrict our analysis to faunas from the skeletal bank habitat, which was the best and most evenly sampled Glen Dean environment (see Fig. 4.4). Over 90% of Appalachian Basin skeletal bank taxa co-occur in the skeletal bank of the Glen Dean sequence in the Illinois Basin, where they account for 95% of the entire sampled fauna (see Table 4.2). The Jaccard Coefficient suggests a relatively lower level of turnover among faunas from the skeletal bank environment ($S_j$ = 0.87), than when faunas were compared on the whole across the two study regions (Table 4.2). Furthermore, lists of the most abundant taxa from both regions exhibit a very high degree of overlap. The ranks of taxa that comprise 90% of each basin's skeletal bank fauna (fenestrate, rhabdomesid, trepostome, and fistuliporid bryozoans) are almost identical, although the abundances of these taxa vary somewhat between basins (Table 4.4). Finally, ANOSIM test results indicate that regional skeletal bank assemblages are barely distinguishable ($R$=0.03; $p$=0.262).

**Between Sequence Turnover**

Rarefaction analyses indicate that taxonomic diversity decreased slightly, but significantly, in the Appalachian Basin from 25.8 taxa in the Haney sequence to 23 taxa

in the Glen Dean sequence (Fig. 4.9A). Percent carryover/holdover and Jaccard Coefficient turnover metrics ($S_j$ = 0.79), suggest that eustatic changes between the Haney and Glen Dean sequence produced little faunal turnover in the Appalachian Basin (Table 4.5). Over 81% of Haney taxa persisted into the Glen Dean sequence, where they accounted for about 97% of the total pool of Glen Dean taxa. ANOSIM tests for faunal differences between these sequences support these findings and indicate that Haney and Glen Dean assemblages are barely distinguishable in the Appalachian basin ($R$=0.13; $p$=<0.001). An analysis of faunal turnover between faunas from the skeletal bank environment (the most evenly sample environment in the Haney and Glen Dean sequences) produces comparable results. Very little faunal turnover occurred with the skeletal bank environment through time ($S_j$ = 0.70), although the amount of turnover exhibited was relatively higher than that shown between the Haney and Glen Dean faunas as a whole (Table 4.5). Ninety percent of Haney skeletal bank taxa recurred in the skeletal bank environment in the Glen Dean sequence, where they accounted for about 82% of the skeletal bank fauna. The ANOSIM test for faunal differences between skeletal bank faunas indicates that they also were nearly indistinguishable ($R$=0.23; $p$=<0.001).

Comparison with the Illinois Basin

Patterns of faunal turnover between the Haney and Glen Dean sequences in the Appalachian Basin share a number of similarities to those observed between these sequences in the Illinois Basin, these include: (1) an equally low level of compositional turnover between sequences when whole faunas and skeletal bank faunas are examined.

This is illustrated in Table 4.5 by Jaccard Coefficient values ($S_j$ whole fauna= 0.80; $S_j$ skeletal bank fauna= 0.70, respectively) and the high percentage of carryover taxa (whole fauna = 92.8%; skeletal bank fauna = 83.3%, respectively) and holdover taxa (whole fauna = 86.7%; skeletal bank fauna = 95.2%, respectively); and (2) comparable results from ANOSIM tests for differences between sequences, which indicate that that Haney and Glen Dean assemblages are barely distinguishable ($R$=0.05; $p$=0.06; $R$=0.19; $p$=0.002, respectively). The only major difference in temporal turnover patterns between basins concerns diversity change. Rarefaction suggests that, unlike diversity in the Appalachian Basin, mean sequence diversity failed to change significantly between the Haney and Glen Dean sequences (28 and 28.6 taxa, respectively) in the Illinois Basin at a sample size of 2900 individuals (Fig. 4.9B).

## Discussion

### Within Sequence Faunal Variability

The results from within sequence comparisons of taxonomic richness, faunal composition, biotic gradients, and geographic turnover indicate only minor variability between regional biotas. Because taxonomic richness, extinction, and diversification are linked to many factors that would be expected to vary locally or regionally, such as availability of resources, nutrients, habitat complexity, presence of predators, etc. (Bambach 1993, Brown 1995, Vermeij and Leighton 2003), we find it surprising that greater faunal differences were not observed in either sequence between these two regions, which are separated by over 300 km. Unfortunately, there have been few studies

which have quantified faunal variability over comparable spatial scales within a discrete time interval, and no studies have yet attempted this using faunas from two separate basins; thus comparisons of our results with those from other studies are difficult. However, limited comparisons can be made. In a quantitative study of a Middle Devonian coral and brachiopod-rich assemblage from a single basin, the Appalachian Basin, Bonelli et al. (2006) reported high levels of faunal change across geographic distances that were comparable to that in the present study (~ 300 km). Using a combination of univariate and multivariate tests, these authors reported significant differences in the composition and structure of communities across the study area, even though samples were collected from a single depositional environment. As additional evidence, Bonelli et al. (2006) cited results from ANOSIM tests, which indicated that assemblages differed clearly with geography (*R* values ranged from 0.57 to 0.65). Thus, in relation to Bonelli et al. (2006) our results indicate substantially less faunal differentiation (ANOSIM $R = 0.36$ and 0.14, for the Haney and Glen Dean sequences respectively), despite the fact that our comparisons were made between faunas in different depositional basins.

The low levels of within sequence faunal variability that we observed may be related to the fact that the Appalachian and Illinois Basins were not entirely separated from one another during the Chesterian. As stated earlier, the Cumberland Saddle provided an open passageway between these regions throughout the study interval. Our results suggest that populations of the same taxa were present within both depositional basins. It is likely, given the communication between basins, that these populations could disperse larvae between regions and perhaps even migrate between regions over time.

Thus, each regional ecosystem and its local communities could have drawn members from essentially the same pool of taxa (cf Jackson 1994, Jackson 1995, Jackson et al. 1996, Pandolfi 1996). Furthermore, because each basin contained a similar array of depositional environments, and, presumably, comparable physical conditions within those habitats (see Geologic Background), taxa should have been able to persist largely undisrupted across regions. Fluctuations in the abundances of particular species or in the overall dominance rankings of taxa, such as those observed in the Haney sequence (see Table 4.1), would not be unexpected in this scenario, as shifting taxon abundances may be associated with minor environmental differences from basin to basin, or due to differences in the interactions of taxa between basins. Together, these features may easily explain the within sequence faunal similarities that we observed.

Relation to Global Faunal Patterns

Previous studies of global macroevolutionary trends during the LPIA indicate that endemic taxa were relatively uncommon during the LPIA interval and that the marine realm was dominated by taxa that had broad geographic distributions (Powell 2005, 2007). These global patterns imply very low levels of faunal turnover (beta diversity) between regions. The results from this chapter support these global findings and indicate that taxa were indeed broadly distributed across the Appalachian and Illinois basins, at least during the interval studied here. However, as discussed above, we attribute this finding to purely regional phenomena, namely the similarity of depositional settings in each basin and the open communication existing between basins. Whether or not faunal turnover is low between other basins remains to be seen, but this question is begging for

future study to better understand the geographic complexity of faunal responses during the LPIA (see Future Work).

**Geographic Variability in Temporal Turnover**

In addition to finding low levels of faunal turnover within a sequence between regions, we also observed comparable and low levels of turnover through time, across an interval of major glacio-eustatic change. Thus, the results from this study suggest that the biotic response to the environmental changes that occurred during the LPIA may have been far less spatially dynamic than we posited in earlier chapters. Although we feel it is unlikely, this could imply that local and regional processes played minor roles in producing patterns of ecosystem persistence or change during the LPIA interval. Given that the middle Carboniferous is widely known to mark the onset of major stratigraphic and lithologic changes across the globe (e.g. Wanless and Shepard 1936, Swann 1964, Frakes and Crowell 1969, 1970, Crowell and Frakes 1971a, 1971b, Frakes et al. 1971, Crowell and Frakes 1975, Frakes et al. 1975, Crowell 1978, Caputo and Crowell 1985, Saunders and Ramsbottom 1986, Veevers and Powell 1987, Walkden 1987, Dickinson et al. 1994, Gonzalez-Bonorino and Eyles 1995, Lopez-Gamundi 1997, Miller and Eriksson 1999, Smith and Read 2000, Wright and Vanstone 2001, Al-Tawil and Read 2003, Cecil et al. 2003, Butts 2005), it may not be unreasonable to suggest that the magnitude and timing of faunal responses to glacio-eustatic changes would be similar in disparate geographic regions during the LPIA.

Importantly however, we suggest that the presence of comparable regional conditions in the Illinois and Appalachian basins played a primary role in driving similar

biotic responses in each region. For example, both regions were comprised of dominantly deeper water facies during the study interval, because increased rates of subsidence caused carbonate ramps to deepen in both basins during the late Chesterian. Deeper water habitats tend to be less prone to environmental fluctuations in general and are thought to provide taxa with stable physical conditions (Bambach 1977, Kowalewski et al. 2002, Scarponi and Kowalewski 2007). Thus, one potential explanation for the low levels of temporal turnover observed in each basin is that the sampled deeper water assemblages were largely buffered from changes that could occur in shallow water settings during glacio-eustatic fluctuations, such as restricted circulation and increased variability in water temperature and salinity during regressions (Hallam 1978). In this context, we find it interesting that levels of diversity decreased to a greater degree from the Haney to Glen Dean sequence within the Appalachian Basin, since it is thought to have been a shallower basin overall and may have been more severely affected by eustatic changes (Nelson et al. 2002, Al-Tawil et al. 2003). Undoubtedly future work is needed to better test this hypothesis, specifically with regards to estimating the magnitudes of eustatic fluctuations between the studied sequences in the Appalachian Basin.

**Implications for Spatial Patterns of Diversity and Turnover During the LPIA**

Although the temporal scope of this study is too restricted to address differences in global and regional faunal patterns of diversity and turnover across the onset of the LPIA, this study provides important insight into the processes that govern geographic diversity and turnover during the LPIA interval. Previous studies of global diversity and

biogeography during the LPIA interval have tended to favor global climate change (primarily increased seasonality) as the main driver of diversity and biogeographical patterns throughout the ice age (Powell 2005, 2007). These studies imply that compiled LPIA global diversity curves are capturing and fairly representing patterns present across all latitudes, paleocontinents, and regions and that biotic patterns are driven by a single global mechanism (the extinction of endemic taxa and the subsequent profileration of taxa with broad geographic distributions). While we agree that our results support the notion that faunal diversity and turnover may have varied little globally (although this pattern must be further scrutinized, see Future Work), we suggest that our observed regional faunal patterns were linked to factors that would be expected to vary spatially across the globe (i.e., habitat availability, regional tectonic history). Thus, it is evident to us that global diversity curves for the LPIA may be masking regional variability that can be observed through detailed regional studies, or as this study has shown, are at least leading to overly-simplified explanations for spatial patterns of faunal diversity and turnover.

## Future Work

This study examines patterns of geographic variability for the broader purpose of gaining a better understanding of the spatial patterns and drivers of biotic turnover within the tropics, during the LPIA. We feel strongly that to better understand the meaning of global LPIA biotic curves additional regional studies are needed that aim to resolve spatial complexity in faunal patterns across the globe. In the following paragraphs, we outline an agenda for future research in this area.

Study Within the Appalachian Basin

In this chapter we examined geographic complexity in biotic patterns at high resolution across only a single eustatic event. However, the Appalachian Basin records 10 other consecutive Chesterian eustatic cycles that span the onset of the LPIA and which have been correlated into the Illinois Basin. Future work could concentrate on resolving how biofacies, regional diversity, faunal turnover, and biotic gradients vary between the Illinois and Appalachian basins further, within and across these other depositional sequences. These additional comparisons would broaden greatly the understanding of geographic variability in faunal patterns between these two basins and also provide important points of comparison against which the results of the current study can be compared. For example, such a study would indicate whether the large-scale changes in the overall abundance structure of regional Haney faunas are typical, or instead, if less structural variation (such as that observed between regional Glen Dean faunas) is the norm. Furthermore, additional work should focus on examining how sequence diversity and biotic composition and structure vary across the onset of the LPIA within the Appalachian Basin to provide an additional regional data point that can be used to compare against patterns shown in the global diversity curves published by Stanley and Powell (2003).

Research Outside of the Study Area

Future research could also investigate Chesterian biotic patterns within and across a number of other regions spread across the globe. Recent work by Izart et al. (2003) has

focused on using sequence stratigraphy to correlate large-scale Carboniferous and Permian depositional sequences across sedimentary basins in Gondwanaland, eastern and western Europe, north Africa, Arabia, China, and North America. Studies such as this can be used to construct regional and interregional stratigraphic frameworks within which paleoecologists can scrutinize, at a high resolution, biotic patterns within and between basins during the LPIA. Given that global level studies suggest that tropical faunas experienced the greatest losses during the LPIA (Stanley and Powell 2003; Powell 2005, 2007), future research could concentrate on investigating and comparing the biotic response to the onset of the LPIA and associated environmental changes within other tropical basins, such as the Midcontinent, Western Interior, and Paradox basins and the Arrow Canyon Range in the US, the Craven Basin of Great Britain, and the Donets Basin of Russia. Furthermore, a second and perhaps more interesting set of comparisons could be made by examining whether the biotic response to the LPIA differed within basins situated at higher latitudes by examining Chesterian deposits from Queensland and New South Wales in eastern Australia or from the Parana′ Basin of South America.

We feel strongly that regional assessments of biotas across the globe will reveal great heterogeneity in how, when, and why regional biotas responded to environmental fluctuations during the LPIA. We believe that the research agenda that we have outlined above will greatly enrich our understanding of the biotic consequences of the LPIA and that global signals, if they indeed exist, will emerge from the study of these regional patterns.

## Conclusions

The major findings of our study can be summarized as follows:

1. There is a high level of faunal similarity between the biotas recovered from the Haney depositional sequence in the Appalachian and Illinois basin regions. For example, despite being separated by over 300 km, these regional Haney faunas have statistically indistinguishable taxonomic diversities and share approximately 89% of their respective taxa. Furthermore, analyses of biotic gradients reveal only minor changes to the composition and structure of Haney faunas between basins. In both regions, biofacies are similar and arrayed along a primary gradient of water depth. Depositional environments and taxa tend to sort along this gradient with high fidelity and similar sets of taxa dominate each region, although the relative abundances of taxa vary geographically. Overall, ANOSIM tests show that regional Haney faunas overlap strongly ($R = 0.36$).
2. Faunas from the Glen Dean sequence of the Appalachian and Illinois basin regions are also highly comparable. One hundred percent of the Appalachian Basin Glen Dean fauna is present within the Illinois Basin. However, regional diversity is narrowly, but significantly, higher in the Illinois Basin region, due to the increased presence of many rare taxa. Despite this, the overall composition and structure of Appalachian and Illinois Basin biotic gradients are very similar. Fenestrate bryozoan dominated biofacies are overwhelmingly important in both regions and arrayed along comparable water depth gradients. Ordination analyses indicate that depositional environments and taxa tend to sort consistently along this gradient in both regions.

Finally, although the percent abundances of the most dominant taxa shift slightly between basins, the ranks of these taxa are nearly identical. ANOSIM results indicate that regional Glen Dean faunas can barely be distinguished from one another ($R$=0.14).

3. An analysis of faunal turnover between the Haney and Glen Dean sequences shows comparable patterns in both basins. Jaccard Coefficient turnover values are very similar between the Haney and Glen Dean sequences in the Appalachian and Illinois basins ($S_j$ = 0.79 and $S_j$ = 0.81, respectively), as are percent carryover metrics (81.5% and 92.8%, respectively), percent holdover metrics (95.7% and 86.7%, respectively) and ANOSIM test results ($R$ = 0.05 and $R$ = 0.13, respectively).
4. Overall the results from this study indicate that faunas from the Haney and Glen Dean sequences do not vary to a large degree geographically between basins; furthermore there also appears to be only minor regional variation in the level of faunal turnover exhibited between these two glacio-eustatic sequences. We suggest that the overall similarity of faunal patterns in each region can be explained regional phenomena: a) the presence of an open passageway between the Appalachian and Illinois basins, which would permit for the exchange of taxa between regions; and b) the existence of a similar suite of depositional environments and environmental conditions in each basin, which happened to buffer taxa from major habitat fluctuations.

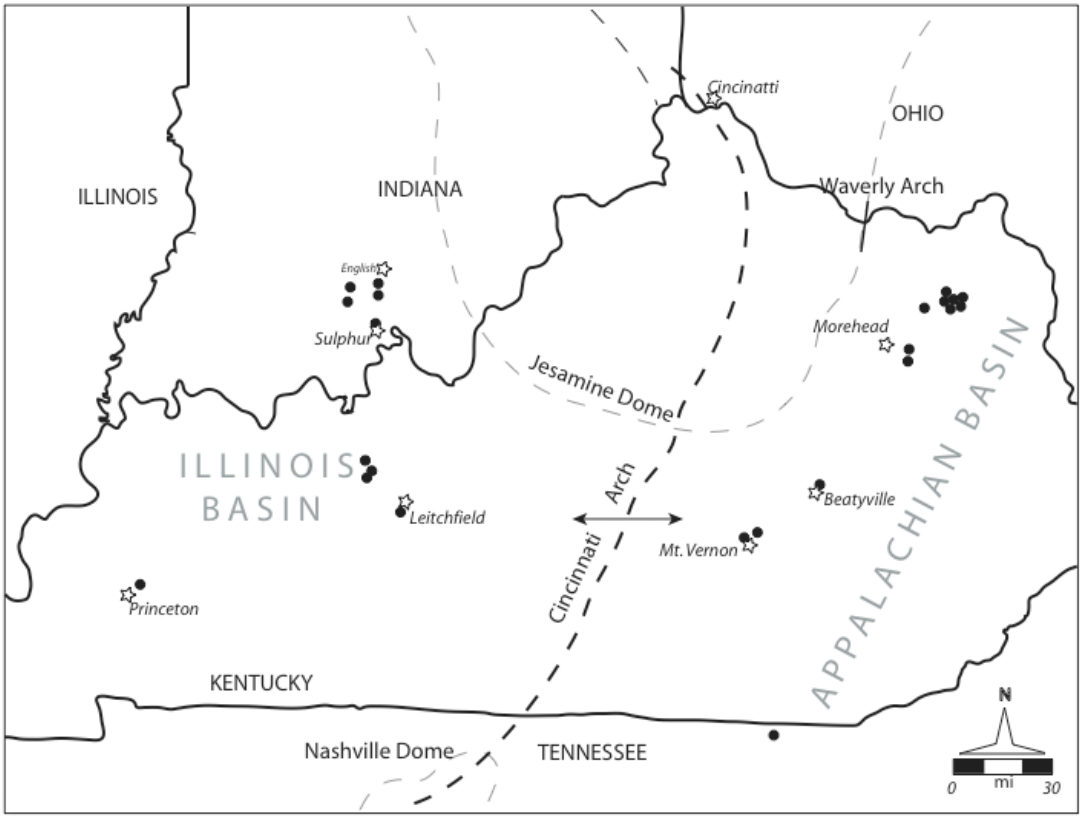



**Figure 4.1. Map of the study area. Black dots represent sampling localities. Bold dashed line represents the Cincinnati Arch. Normal dashed lines represent the Jesamine Dome (top) and Nashville Dome (bottom). Double-sided arrow represents the Cumberland Saddle, an open passageway between the Illinois and Appalachian basins.**

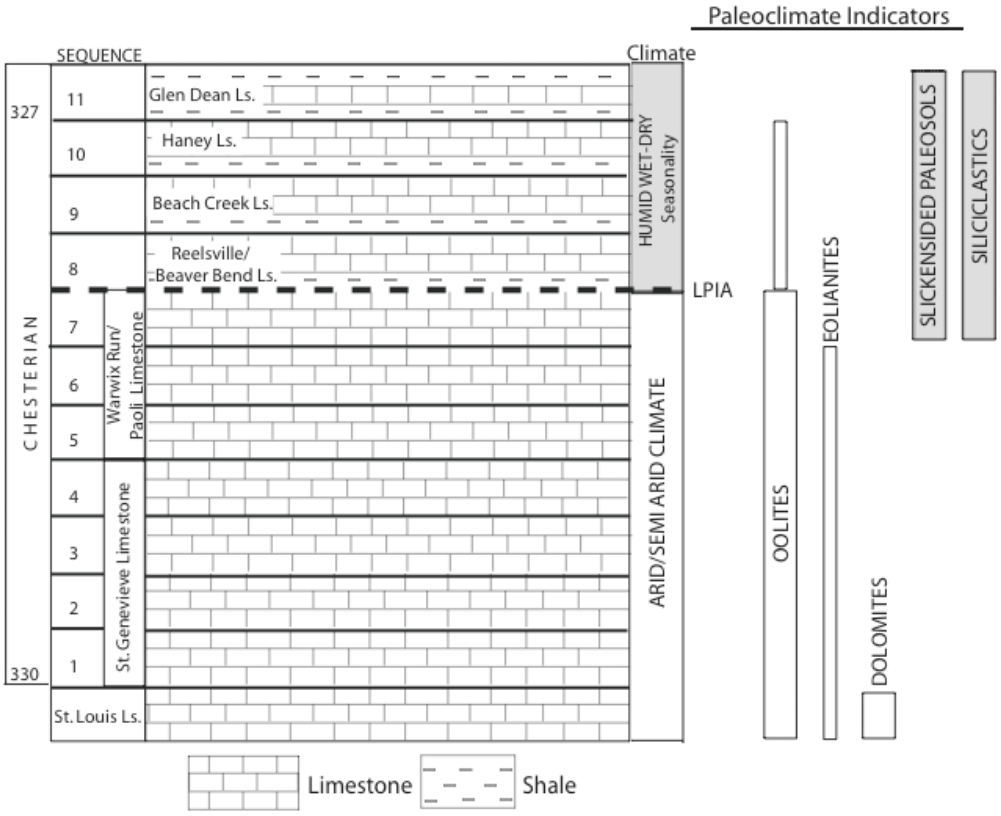



**Figure 4.2. Depositional sequences, inferred paleoclimate, and paleoclimatic indicators for the study interval in the Appalachian Basin. Bold dotted line represents onset of LPIA.**

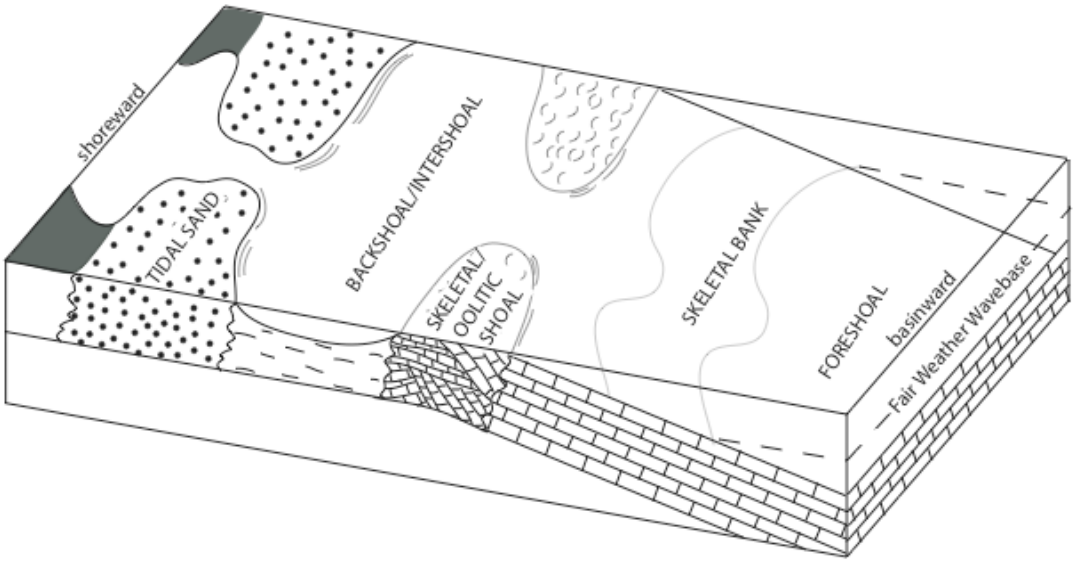
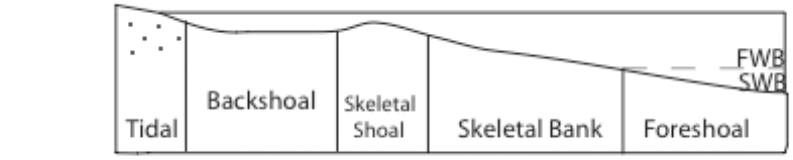



**Figure 4.3. Schematic representation of the depositional environments sampled in this study.**




| | | Tidal | Backshoal | Skeletal Shoal | Skeletal Bank | Foreshoal | *Total Samples Collected* | *Total Individuals Collected* |
|---|---|---|---|---|---|---|---|---|
| Glen Dean Fm. | **I.B.** | | 8 | 11 | 14 | | 33 | 3162 |
| | **A.B.** | | 2 | | 13 | 11 | 26 | 1947 |
| Haney Fm. | **I.B.** | 24 | 4 | 4 | 10 | 4 | 46 | 2947 |
| | **A.B.** | 4 | | | 14 | 30 | 48 | 1989 |

**Figure 4.4. Time-environment plot of number of samples grouped by depositional sequence and environment. A.B. represents Appalachian Basin, I.B. represents Illinois Basin. FWB represents fair weather wave base, SWB represents storm wave base.**

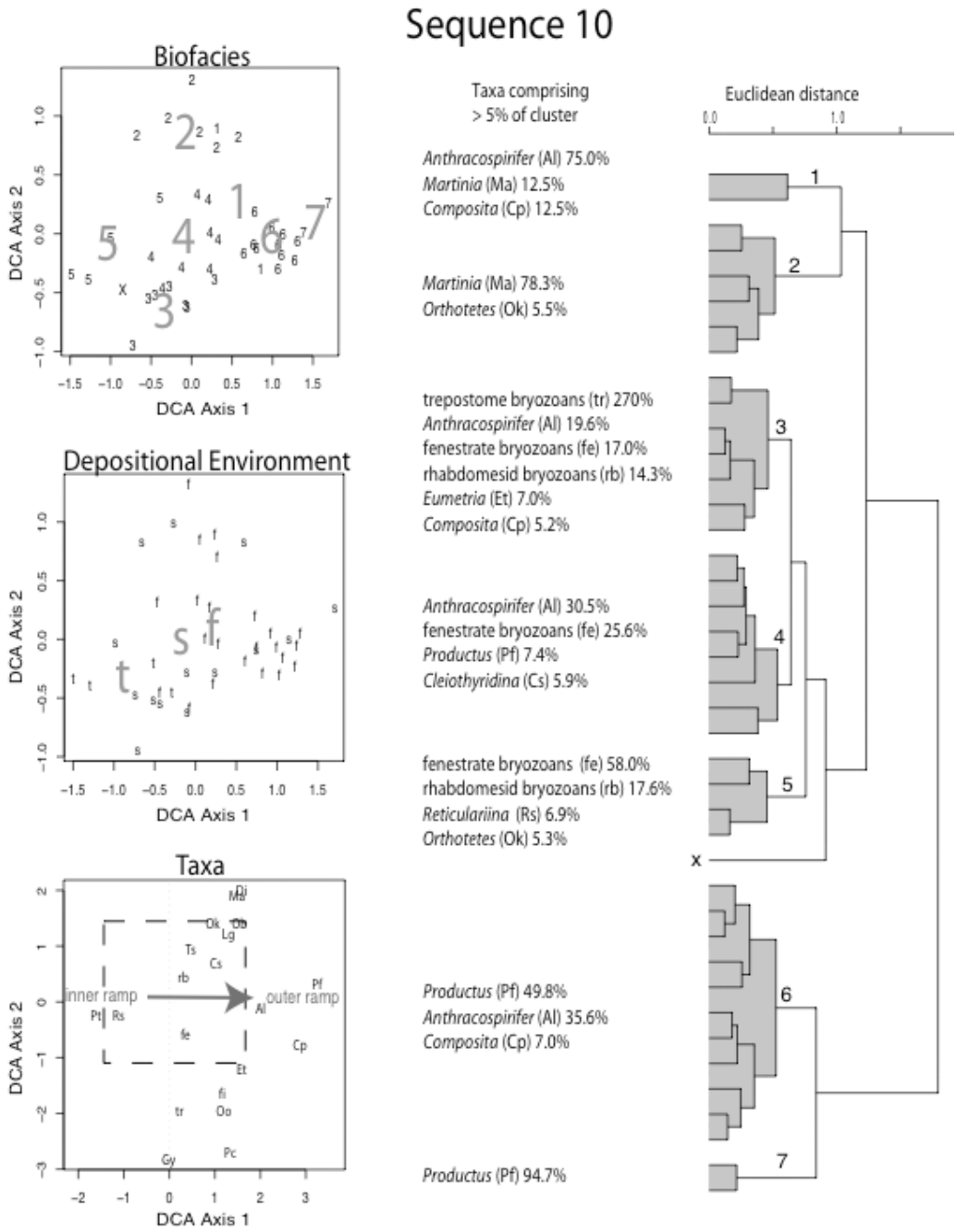



**Figure 4.5. Results from cluster analysis and ordination of Haney Formation. Cluster dendrogram is shown at right, with percent composition of each biofacies shown for taxa comprising more than 5% of the individuals from the biofacies. DCA results are displayed at left, with sample scores plotted by biofacies membership (top), depositional environment (middle), and taxon scores (bottom). The dashed box in the taxon plot delineates the area within which sample scores plot. t = tidal flat; b=backshoal; s= skeletal bank; f = foreshoal; x = sample outliers in cluster analysis. Small type in DCA plots corresponds to individual samples; large type indicates biofacies and depositional environment centroids. Two-letter taxon codes are displayed in Table 4.6. Cluster analysis agglomerative coefficient is 0.85.**

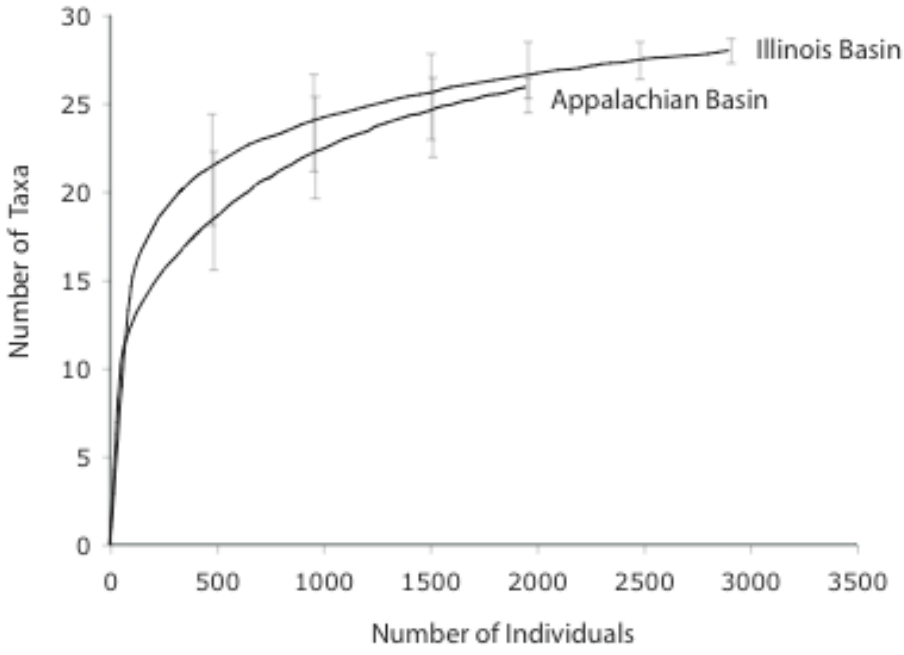



**Figure 4.6. Rarefaction curves displaying the taxonomic diversity of the Haney sequence in the Appalachian Basin and Illinois Basin. Confidence intervals are 95% confidence intervals.**

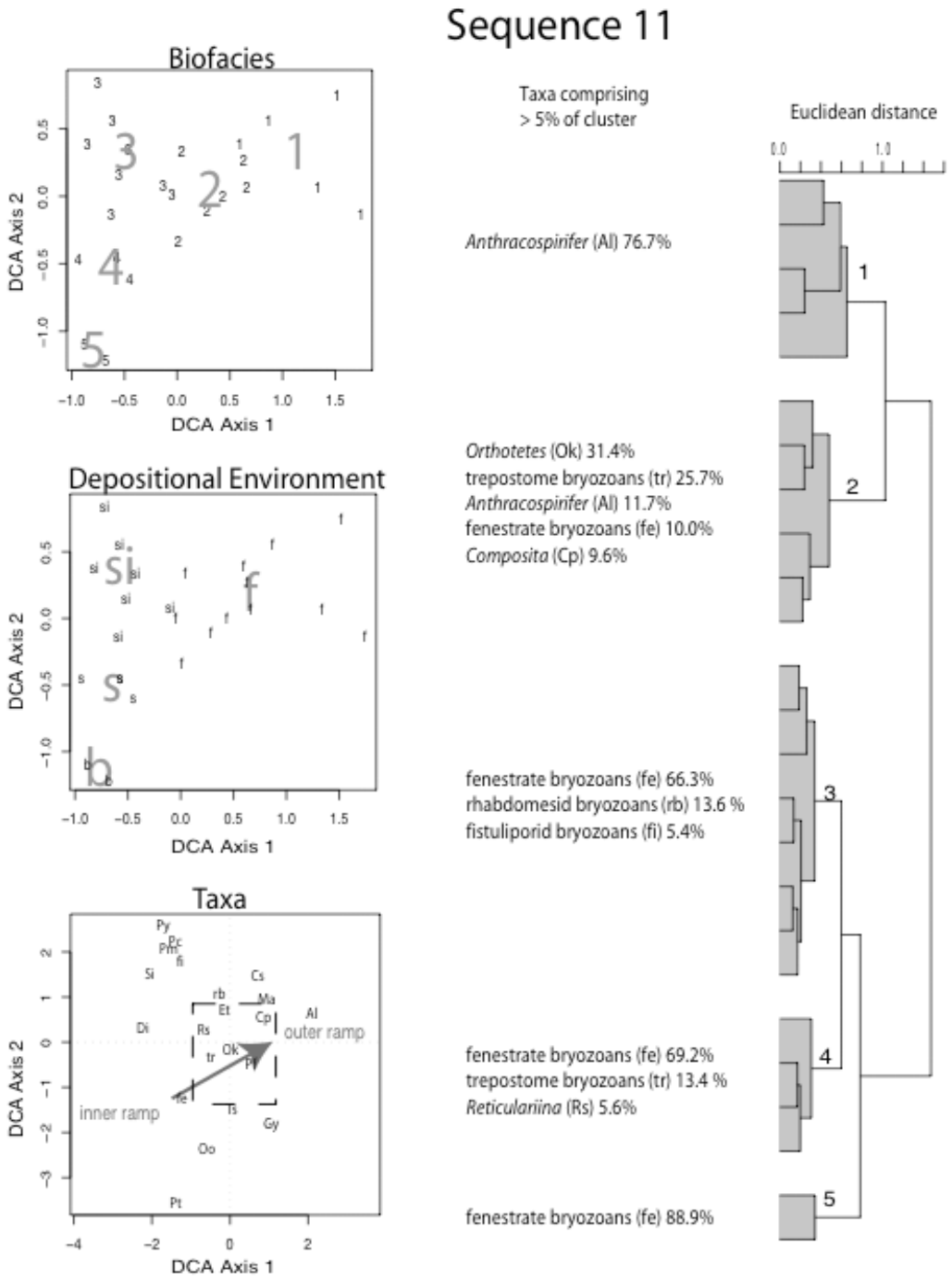



**Figure 4.7. Results from cluster analysis and ordination of Glen Dean Formation. Cluster analysis agglomerative coefficient is 0.83. See figure 4.5 caption for description of text symbols. See Table 4.6 for taxon codes.**

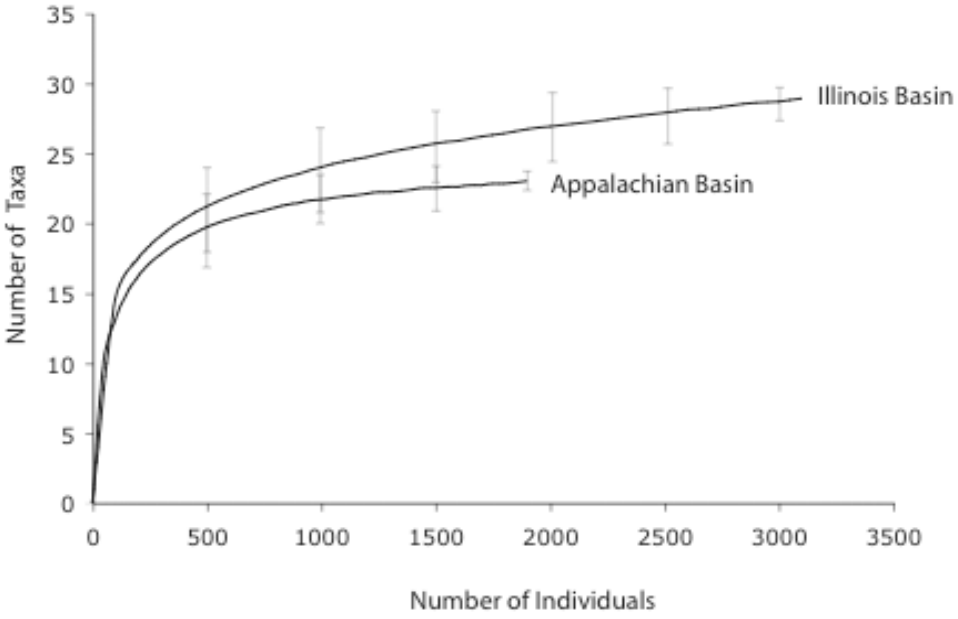



**Figure 4.8. Rarefaction curves displaying the taxonomic diversity of the Glen Dean sequence in the Appalachian Basin and Illinois Basin. Confidence intervals are 95% confidence intervals.**

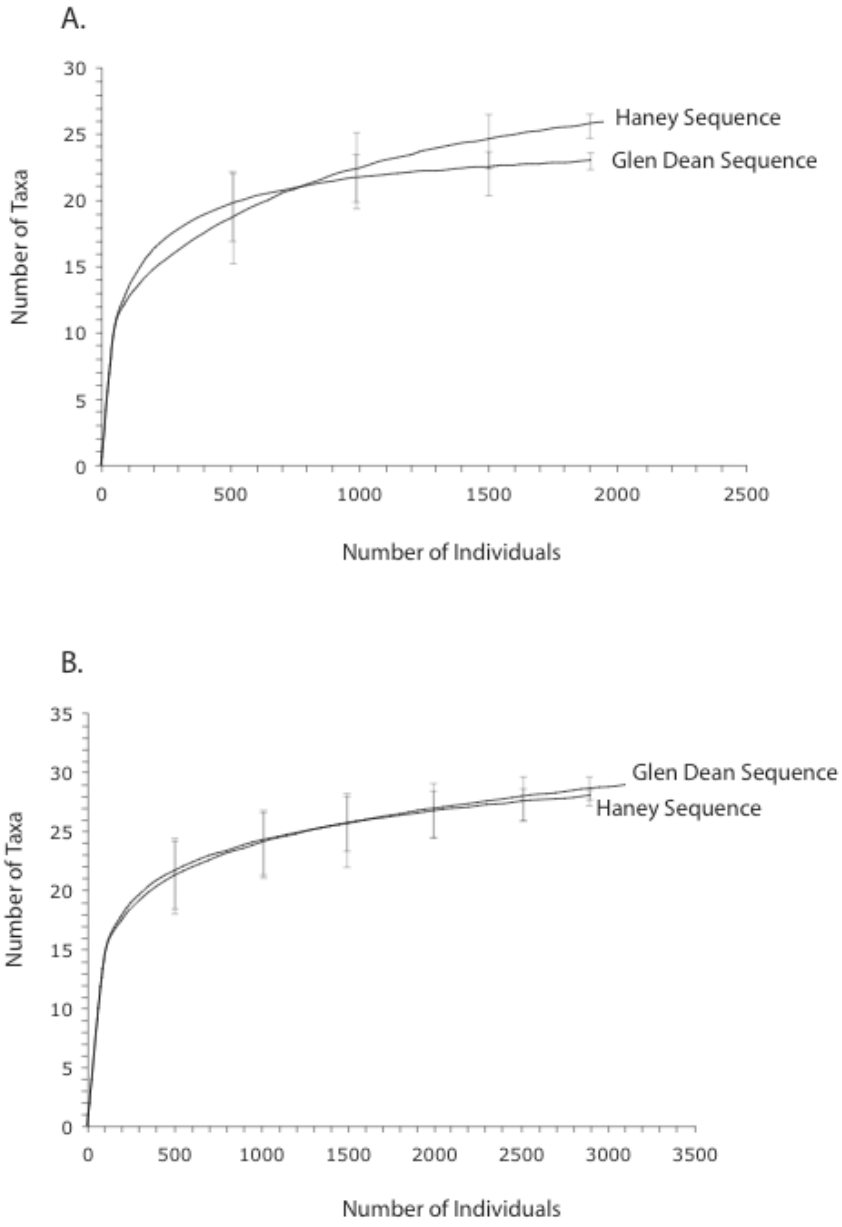



**Figure 4.9. Rarefaction curves displaying the taxonomic diversity of the Haney and Glen Dean formations for: (A) the Appalachian Basin (B) the Illinois Basin. Confidence intervals are 95% confidence intervals.**

| Appalachian Basin | | Illinois Basin | |
|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance |
| *Anthracospirifer* | 22.4 | fenestrate bryozoans | 57.0 |
| *Martinia* | 22.4 | rhabdomesid bryozoans | 9.2 |
| *Productus* | 18.2 | *Productus* | 6.7 |
| fenestrate bryozoans | 14.1 | trepostome bryozoans | 5.2 |
| rhabdomesid bryozoans | 5.0 | fistuliporid bryozoans | 3.9 |
| trepostome bryozoans | 5.0 | *Reticulariina* | 3.1 |
| *Composita* | 3.0 | *Pentremites* | 2.5 |
| *Eumetria* | 2.9 | *Composita* | 1.9 |
| | | *Cleiothyridina* | 1.5 |

**Table 4.1. Lists of the taxa comprising up to 90% of the individulas collected from the Haney sequence in the Appalachian and Illinois Basins, respectively.**

| Data Set | % Carryover | % Holdover | Turnover (Jaccard Coefficient) |
|---|---|---|---|
| Haney whole fauna | 88.9 | 85.7 | 0.77 |
| Haney skeletal bank fauna | 85.0 | 70.8 | 0.63 |
| Glen Dean whole fauna | 100.0 | 79.3 | 0.79 |
| Glen Dean skeletal bank fauna | 91.0 | 95.2 | 0.87 |

**Table 4.2. Percent carryover/holdover and Jaccard Coefficient turnover metrics that were calculated to compare within sequence faunal turnover between the Appalachian and Illinois basins.**

| Appalachian Basin (whole fauna) | | Illinois Basin (whole fauna) | |
|---|---|---|---|
| Taxon | Percent Abunance | Taxon | Percent Abunance |
| fenestrate bryozoans | 55.3 | fenestrate bryozoans | 51.0 |
| rhabdomesid bryozoans | 10.0 | rhabdomesid bryozoans | 11.2 |
| *Anthracospirifer* | 7.9 | trepostome bryozoans | 7.4 |
| trepostome bryozoans | 7.0 | *Productus* | 4.7 |
| *Orthotetes* | 5.0 | fistuliporid bryozoans | 4.6 |
| fistuliporid bryozoans | 3.6 | Reticulariina | 3.7 |
| *Eumetria* | 1.7 | Composita | 2.9 |
| | | *Eumetria* | 2.5 |
| | | *Anthracospirifer* | 2.2 |

**Table 4.3. Lists of the taxa comprising up to 90% of the individuals collected from the Glen Dean sequence in the Appalachian and Illinois basins.**

| Appalachian Basin (skeletal bank fauna) | | Illinois Basin (skeletal bank fauna) | |
|---|---|---|---|
| Taxon | Percent Abunance | Taxon | Percent Abunance |
| fenestrate bryozoans | 67.3 | fenestrate bryozoans | 42.7 |
| rhabdomesid bryozoans | 11.8 | rhabdomesid bryozoans | 17.4 |
| trepostome bryozoans | 5.2 | trepostome bryozoans | 12.1 |
| fistuliporid bryozoans | 4.8 | fistuliporid bryozoans | 9.1 |
| *Reticulariina* | 1.7 | *Reticulariina* | 4.6 |
| | | *Composita* | 2.4 |
| | | *Cleiothyridina* | 1.8 |

**Table 4.4. Lists of the taxa comprising up to 90% of the individuals collected from the skeletal bank habitat in the Glen Dean sequence in the Appalachian and Illinois basins.**

| Data Set | % Carryover | % Holdover | Turnover (Jaccard Coefficient) |
|---|---|---|---|
| App. Basin whole fauna | 81.5 | 95.7 | 0.79 |
| App. Basin skeletal bank fauna | 90.0 | 81.2 | 0.70 |
| Illinois Basin whole fauna | 92.8 | 86.7 | 0.81 |
| Illinois Basin skeletal bank fauna | 83.3 | 95.2 | 0.80 |

**Table 4.5. Percent carryover/holdover and Jaccard Coefficient turnover metrics that were calculated to compare faunal turnover between sequences in the Appalachian and Illinois basins.**

| Code | Taxon | Code | Taxon |
|---|---|---|---|
| Al | *Anthracospirfer* | Su | *Schellwienella* |
| Ap | *Athyris* | Si | *Spirifer* |
| Cs | *Cleiothyridina* | To | *Torynifer* |
| Cp | *Composita* | tr | trepostomata |
| Dy | *Dictyoclostus* | Ts | *Triplophyllites* |
| Di | *Dielasma* | | |
| Ea | *Echinochonchus* | | |
| Et | *Eumetria* | | |
| fe | fenestellidae | | |
| fi | fistuliporidae | | |
| Gy | *Girtyella* | | |
| Lm | *Limipecten* | | |
| Lg | *Lingula* | | |
| Ma | *Martinia* | | |
| Ob | *Orbiculoidea* | | |
| Ok | *Orthotetes* | | |
| Oo | *Ovatia* | | |
| Pc | *Paladin* | | |
| Pm | *Pentremites* | | |
| Py | *Platyceras* | | |
| Pf | *Productus* | | |
| Pt | *Punctospirifer* | | |
| Rs | *Reticulariina* | | |
| rb | rhabdomisid | | |

**Table 4.6. Taxon codes used in the ordinations in figures 4.5 and 4.7.**

# Chapter 5. Conclusions

## Linking Global and Regional Biotic Patterns

### Taxonomic and Ecologic Diversity

The results from this study strongly suggest that global level biotic patterns may mask variation that is evident at smaller spatial scales, particularly at the levels of local paleocommunities and regional ecosystems, and may inhibit our understanding of the processes that combine to drive long-term ecological and evolutionary change. In the preceding chapters I have shown that regional diversity remained essentially stationary in the tropical Illinois Basin, among depositional sequences spanning the onset of the LPIA, an interval of major environmental perturbation. The initiation of this global event also failed to produce significant levels of faunal turnover in the Illinois Basin. In contrast, anywhere from 76% to 92% percent of taxa persisted from pre-LPIA sequences into LPIA sequences. Like taxonomic diversity, the diversity of guilds and diversity within guilds also persisted, with little turnover, into the ice age interval, indicating that the ecologic structuring of ecosystems was largely unaffected by the onset of the LPIA. These regional patterns differ substantially from previously documented global patterns, which indicate that 28% of marine genera underwent extinction across the onset of the LPIA (see Stanley and Powell 2003). Therefore, while extinction may have been concentrated within low latitude settings on the whole (see Powell 2005, 2007), the magnitude and/or timing of extinction must have varied geographically among basins situated at low latitudes, as evidenced by the muted response of faunas from the Illinois Basin – which was situated between 5° and 15° south of the equator during the LPIA.

The major physical perturbation associated with the onset of the LPIA within the Illinois Basin was a significant decrease in eustatic sea level, which is manifested across the region as a deeply incised erosion surface (see Smith and Read 2001). One potential reason that Illinois Basin diversity was largely unaffected across the onset of the LPIA is that eustatic sea level falls tend not to produce major extinction events (Jablonski 1985, Valentine and Jablonski 1991, Hallam and Wignall 1997), unless they are significantly long-lived so that preferable habitat conditions fail to be restored (Hallam 1981). Given the relatively quick return to pre-ice age sea levels (within about 350 Kyr; see Smith and Read 2001), it seems likely that taxa were able to persist within (or outside) of the Illinois Basin either by tracking their preferred habitat conditions or persisting in other habitats, until more-favorable conditions returned to the basin.

Biotic Gradients

Unlike taxonomic diversity, regional biotic gradients shifted markedly with the onset of the ice age. The transition to the LPIA coincided with a decrease in the differentiation of faunas among habitats in the Illinois Basin that was tied to an apparent increase in eurytopy. At first glance, these regional trends appear to parallel documented global ecological shifts that occurred during the study interval, such as the increase in the global dominance of eurytopic taxa (Powell 2005, 2007). However, results from Chapter 2 suggest that different processes acted to produce this change at each geographic level. In the Illinois Basin, the increase in eurytopy was driven by an increase in the slope of the basin platform. This created environmentally stable, deeper water habitats that would buffer taxa from physical disturbances, like eustatic fluctuations, which would have a

greater impact in shallower environments (Hallam and Wignall 1997). Deeper water environments tend to contain very weakly defined assemblages, which appear more eurytopic, because of the existence of similar favorable conditions over a broad swath of the carbonate ramp (cf Brett 1998). At the global scale, the increase in the dominance of eurytopes was driven by the global extinction of stenotopic taxa with very restricted latitudinal ranges (Stanley and Powell 2003; Powell 2005, 2007). Thus, despite the similar increase in eurytopy at global and regional levels, unique processes acted to produce the same faunal pattern at each scale. Future work should investigate faunal responses to the onset of the LPIA in other regions to better understand the importance of the processes of global extinction versus local habitat change in driving LPIA faunal patterns.

The apparent increase in eurytopy during the late Paleozoic, by whatever means, may be responsible for perceived differences in the stability of biotic gradients throughout the Paleozoic. Eurytopic taxa tend to have characteristically low rates of origination and extinction, have large geographic ranges, and can tolerate a broad range of environmental conditions (Hansen 1978, 1980, Buzas and Culver 1984, Jablonski 1986, Stanley 1986, Vrba 1987, Norris 1991, 1992, Baumiller 1993, Gili and Martinell 1994, Kammer et al. 1997, McKinney 1997, Kammer et al. 1998). The relative increase in the dominance of eurytopes that occurred at the onset of the LPIA was not a short lived phenomenon, rather eurytopes remained dominant for nearly 50-80 million years – the entire duration of the LPIA (Stanley and Powell 2003; Powell 2005, 2007). Given their propensity for extinction resistance, the increased presence of eurytopes within late Paleozoic ecosystems may explain why late Paleozoic assemblages tend to be more

persistent than those of the early Paleozoic, as outlined in Chapter 2. Detailed regional investigations of biotic gradients are needed from the early and late Paleozoic, to more fully understand the role that eurytopic taxa may have played in driving patterns of Paleozoic faunal stability.

Geographic Variability

The results from Chapter 4 suggest that there was little geographic variability in the response of regional faunas to glacio-eustasy during the early LPIA. However, these results highlight the importance of interpreting regional biotic trends in light of independently recorded regional environmental conditions. Both the Illinois and Appalachian basins contained a similar set of conditions (i.e., widespread deeper water habitats) that may have helped to buffer taxa from the effects of glacio-eustatic change. In addition, these basins were connected to one another, which would allow for migration or larval dispersal between regions. The findings of this chapter do not rule out the possibility that there was much geographic variability in the biotic response to climate and environmental change during the LPIA. Other basins may have harbored different sets of environmental conditions, such as shallower water, more restricted settings, that would be more significantly perturbed by the physical disturbances accompanying the LPIA. Future work is needed which compares the results of this study to those from other basins across the globe, during the LPIA interval. Such a comparison would elucidate whether or not regional patterns in the Illinois and Appalachian Basins are typical and provide an improved understanding for how different regional environmental conditions may have promoted or inhibited extinction during the LPIA interval.

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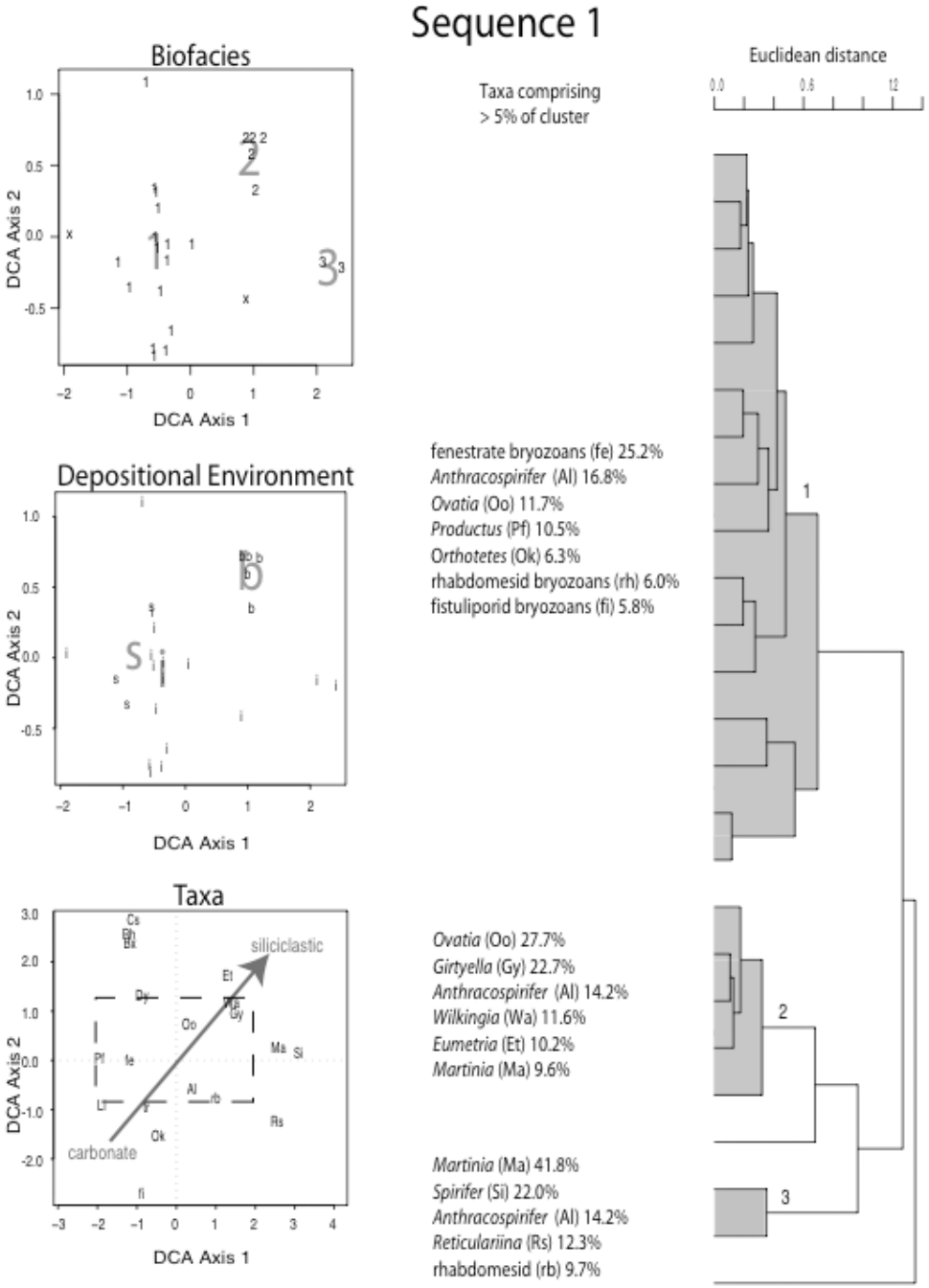
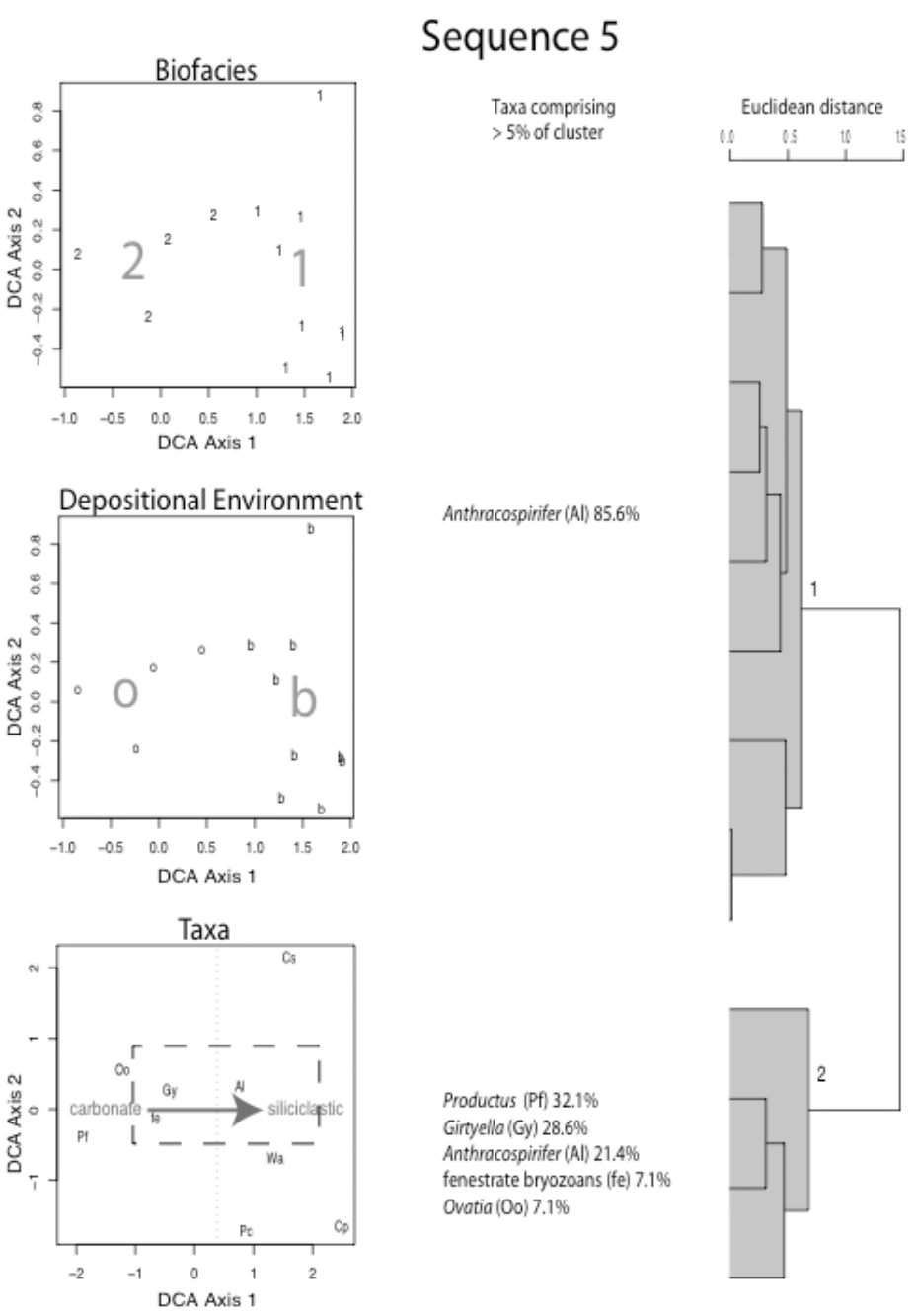
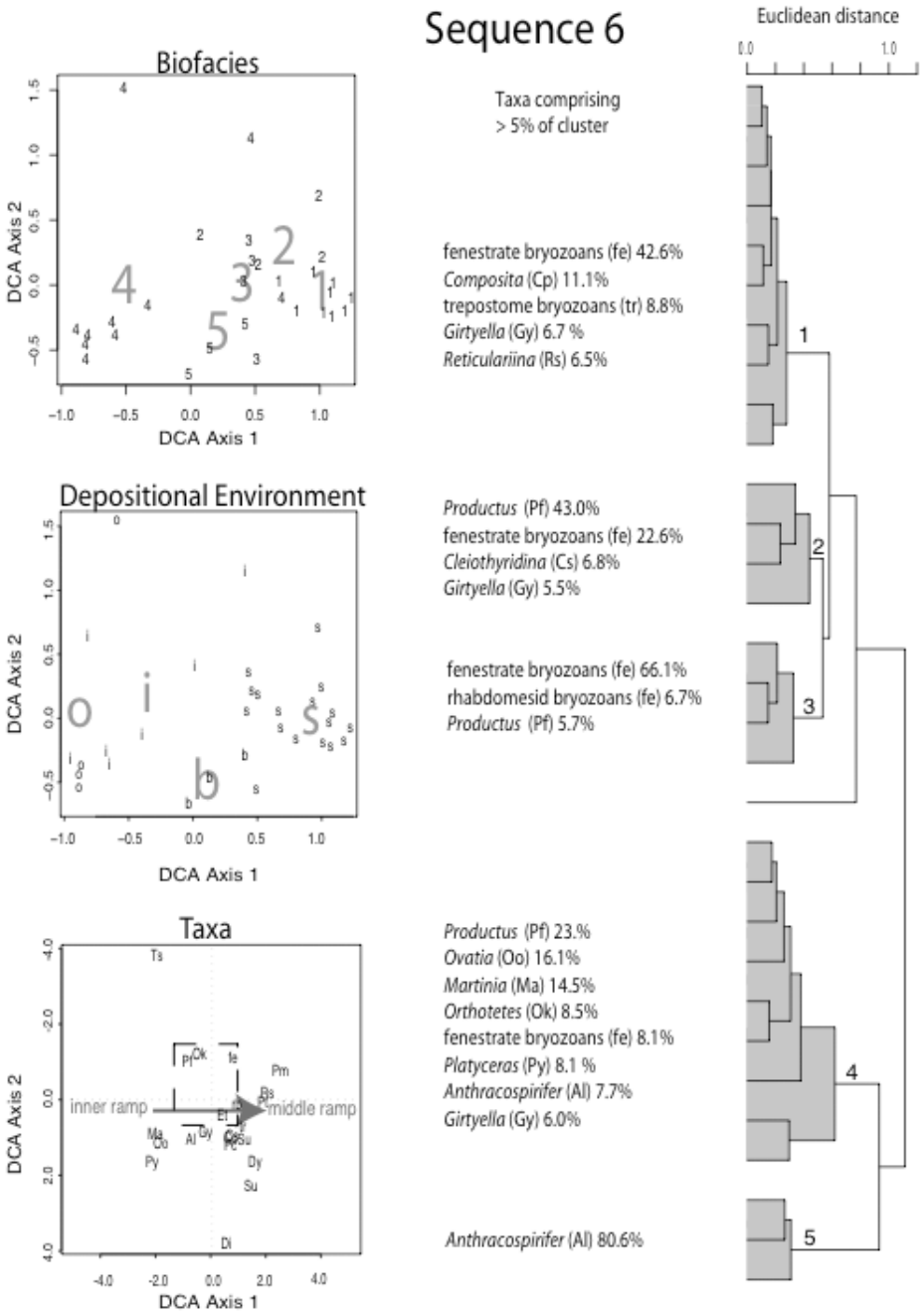
# Appendix A.

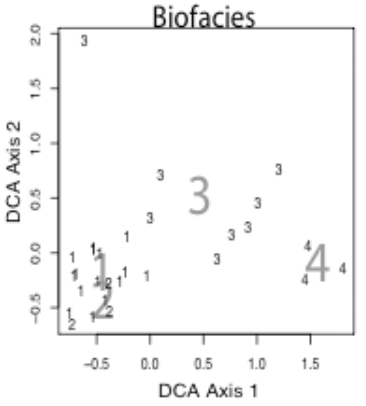
## Biofacies Analyses

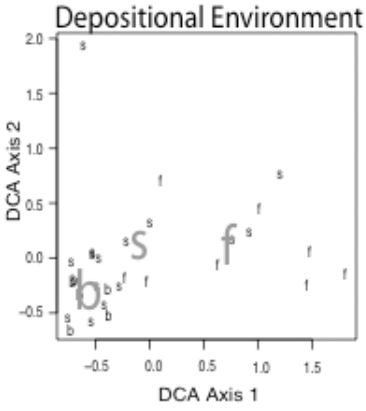
The following figures are from an analysis of biofacies that was conducted as part of Chapter 2. One figure is shown for each depositional sequence. Each figure displays a Q-mode cluster dendrogram (right) with biofacies delineated by numbers. Taxa comprising greater than five percent of the individuals in each biofacies are listed next to the dendrogram and occur in rank order. DCA ordinations with samples coded by biofacies are shown at top; samples are coded by depositional environment in the middle plot. Ordinations of taxa are shown at the bottom. Small type represents the score of an individual sample in ordination space. Bold face type refers to the average sample score of samples comprising a biofacies or depositional environment. The dashed line in the taxa plot corresponds to the total area within which sample scores plot. t = tidal, b = backshoal, i = intershoal, h = skeletal shoal, o = oolitic shoal, s = skeletal bank, f = foreshoal, x = sample outlier as determined by cluster analysis.

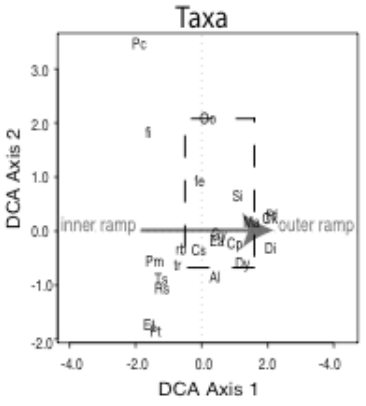

Sequence 1
Biofacies
DCA Axis 2
DCA Axis 1
Depositional Environment
DCA Axis 2
DCA Axis 1
Taxa
siliciclastic
carbonate
DCA Axis 2
DCA Axis 1
Euclidean distance
Taxa comprising
> 5% of cluster
fenestrate bryozoans (fe) 25.2%
Anthracospirifer (Al) 16.8%
Ovatia (Oo) 11.7%
Productus (Pf) 10.5%
Orthotetes (Ok) 6.3%
rhabdomesid bryozoans (rh) 6.0%
fistuliporid bryozoans (fi) 5.8%
Ovatia (Oo) 27.7%
Girtyella (Gy) 22.7%
Anthracospirifer (Al) 14.2%
Wilkingia (Wa) 11.6%
Eumetria (Et) 10.2%
Martinia (Ma) 9.6%
Martinia (Ma) 41.8%
Spirifer (Si) 22.0%
Anthracospirifer (Al) 14.2%
Reticulariina (Rs) 12.3%
rhabdomesid (rb) 9.7%
1
2
3


Sequence 5
Biofacies
DCA Axis 2
DCA Axis 1
Depositional Environment
DCA Axis 2
DCA Axis 1
Taxa
Cs
Oo
Gy
Al
carbonate
siliciclastic
Pf
Ta
Wa
Pc
Cp
DCA Axis 2
DCA Axis 1
Taxa comprising
> 5% of cluster
Euclidean distance
0.0
0.5
1.0
1.5
Anthracospirifer (Al) 85.6%
1
2
Productus (Pf) 32.1%
Girtyella (Gy) 28.6%
Anthracospirifer (Al) 21.4%
fenestrate bryozoans (fe) 7.1%
Ovatia (Oo) 7.1%


Sequence 6
Euclidean distance
0.0
1.0
Biofacies
DCA Axis 2
DCA Axis 1
Taxa comprising
> 5% of cluster
fenestrate bryozoans (fe) 42.6%
Composita (Cp) 11.1%
trepostome bryozoans (tr) 8.8%
Girtyella (Gy) 6.7 %
Reticulariina (Rs) 6.5%
1
Depositional Environment
DCA Axis 2
DCA Axis 1
Productus (Pf) 43.0%
fenestrate bryozoans (fe) 22.6%
Cleiothyridina (Cs) 6.8%
Girtyella (Gy) 5.5%
2
fenestrate bryozoans (fe) 66.1%
rhabdomesid bryozoans (fe) 6.7%
Productus (Pf) 5.7%
3
Taxa
DCA Axis 2
DCA Axis 1
inner ramp
middle ramp
Productus (Pf) 23.%
Ovatia (Oo) 16.1%
Martinia (Ma) 14.5%
Orthotetes (Ok) 8.5%
fenestrate bryozoans (fe) 8.1%
Platyceras (Py) 8.1 %
Anthracospirifer (Al) 7.7%
Girtyella (Gy) 6.0%
4
Anthracospirifer (Al) 80.6%
5

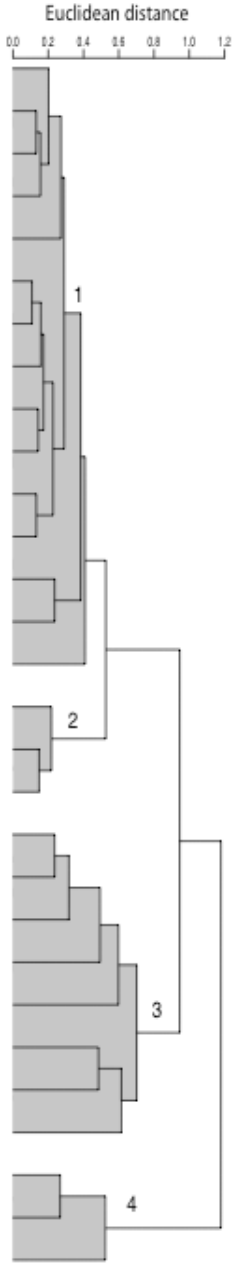



# Sequence 7

Taxa comprising
> 5% of cluster

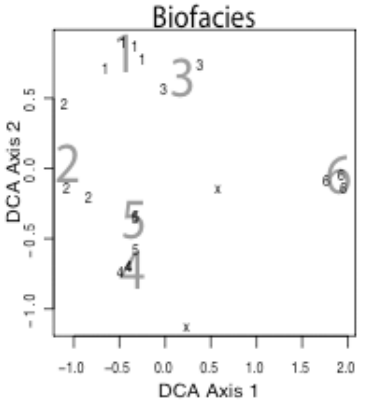


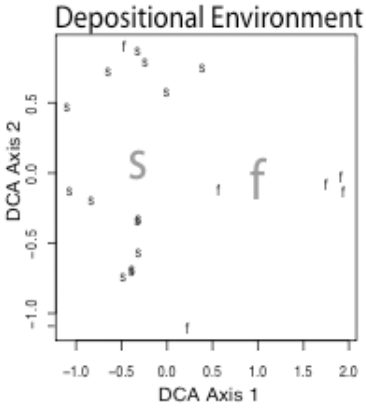

fenestrate bryozoans (fe) 32.0%
*Reticulariina* (Rs) 19.7%
trepostome bryozoans (tr) 14.6%
rhabdomesid bryozoans (rb) 7.5%
fistuliporid bryozoans (fi) 5.8%

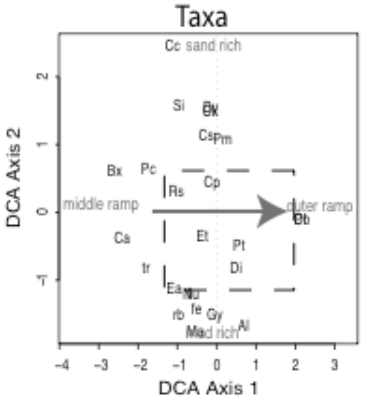
*Reticulariina*(Rs) 69.9%
*Anthracospirifer* (Al) 8.9%
*Eumetria* (Et) 5.6%

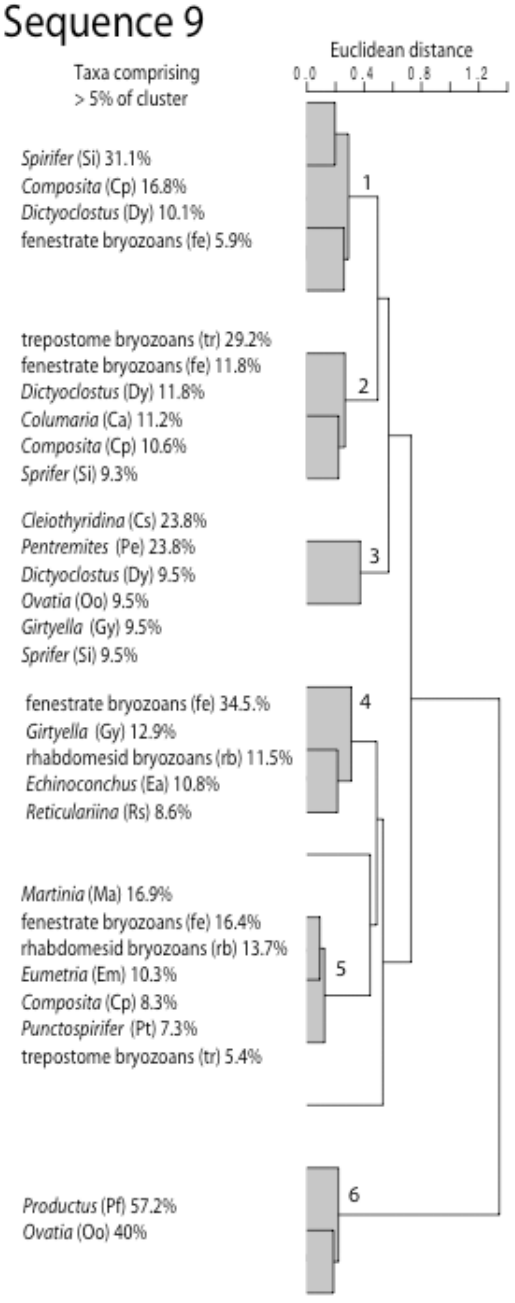
*Martinia* (Ma) 26.4%
fenestrate bryozoan (fe) 17.4%
*Ovatia* (Oo) 14.9%
*Productus* (Pf) 10.5%
*Spirifer* (Si) 10.1%
*Dictyoclostus* (Dy) 7.4%

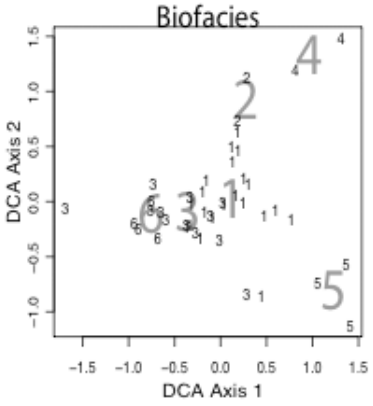
*Productus* (Pf) 69.9%
*Anthracospirifer* (Al) 8.2%
*Dielasma (Di)* 6.8%
Girtyella (Gy) 6.8%
*Dictyoclostus* (Dy) 5.5%

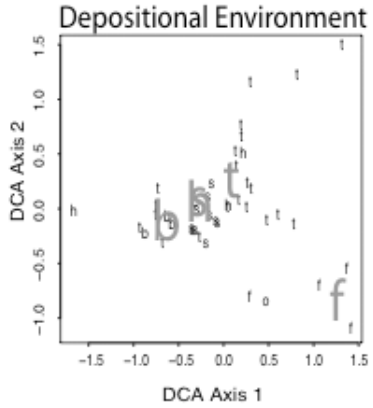

Biofacies
DCA Axis 2
DCA Axis 1

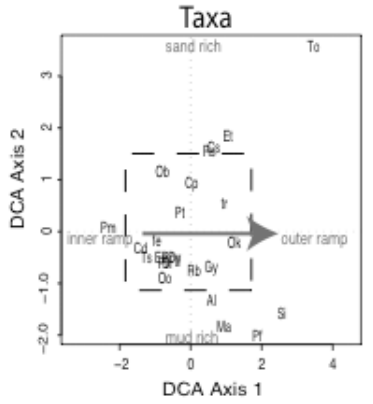

Depositional Environment
DCA Axis 2
DCA Axis 1

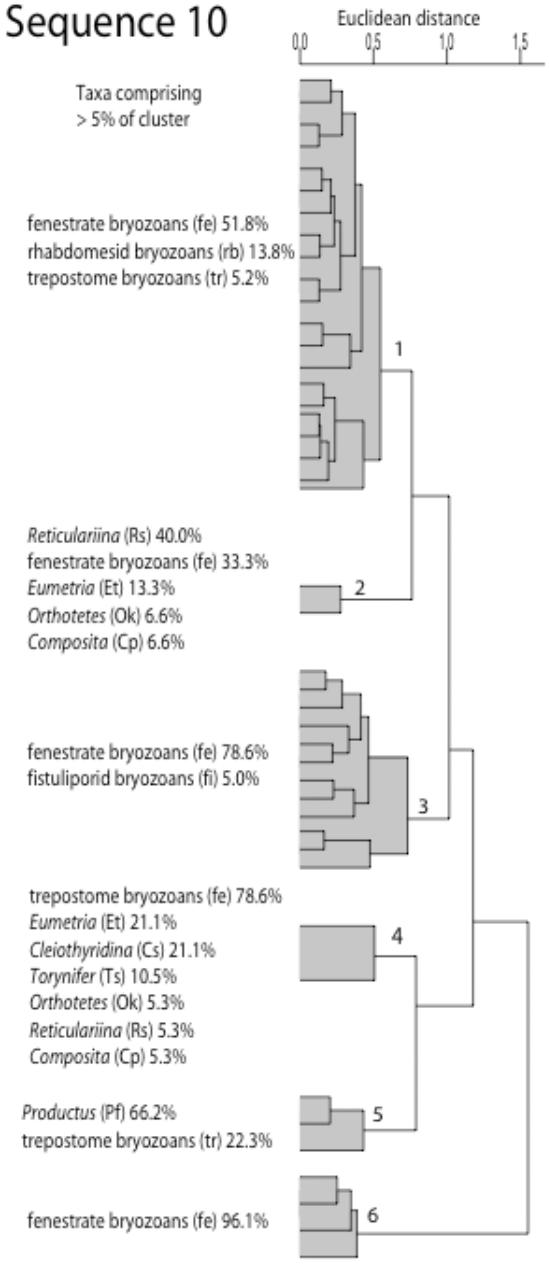

Taxa
Cc sand rich
middle ramp
outer ramp
Ma mud rich
DCA Axis 2
DCA Axis 1

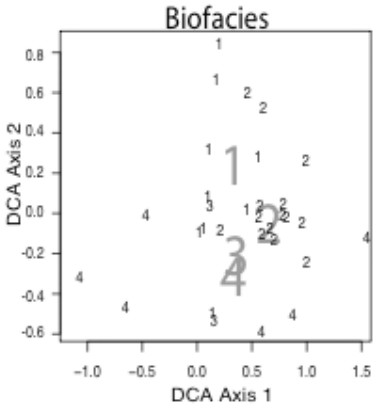

Sequence 9
Taxa comprising
> 5% of cluster
Euclidean distance
0.0
0.4
0.8
1.2
Spirifer (Si) 31.1%
Composita (Cp) 16.8%
Dictyoclostus (Dy) 10.1%
fenestrate bryozoans (fe) 5.9%
1
trepostome bryozoans (tr) 29.2%
fenestrate bryozoans (fe) 11.8%
Dictyoclostus (Dy) 11.8%
Columaria (Ca) 11.2%
Composita (Cp) 10.6%
Sprifer (Si) 9.3%
2
Cleiothyridina (Cs) 23.8%
Pentremites (Pe) 23.8%
Dictyoclostus (Dy) 9.5%
Ovatia (Oo) 9.5%
Girtyella (Gy) 9.5%
Sprifer (Si) 9.5%
3
fenestrate bryozoans (fe) 34.5%
Girtyella (Gy) 12.9%
rhabdomesid bryozoans (rb) 11.5%
Echinoconchus (Ea) 10.8%
Reticulariina (Rs) 8.6%
4
Martinia (Ma) 16.9%
fenestrate bryozoans (fe) 16.4%
rhabdomesid bryozoans (rb) 13.7%
Eumetria (Em) 10.3%
Composita (Cp) 8.3%
Punctospirifer (Pt) 7.3%
trepostome bryozoans (tr) 5.4%
5
Productus (Pf) 57.2%
Ovatia (Oo) 40%
6

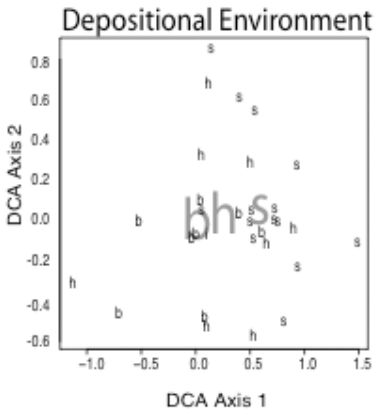

Biofacies
DCA Axis 2
DCA Axis 1

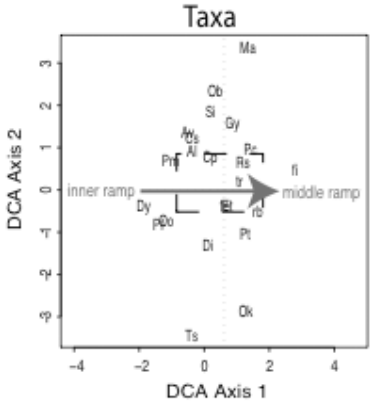

Depositional Environment
DCA Axis 2
DCA Axis 1

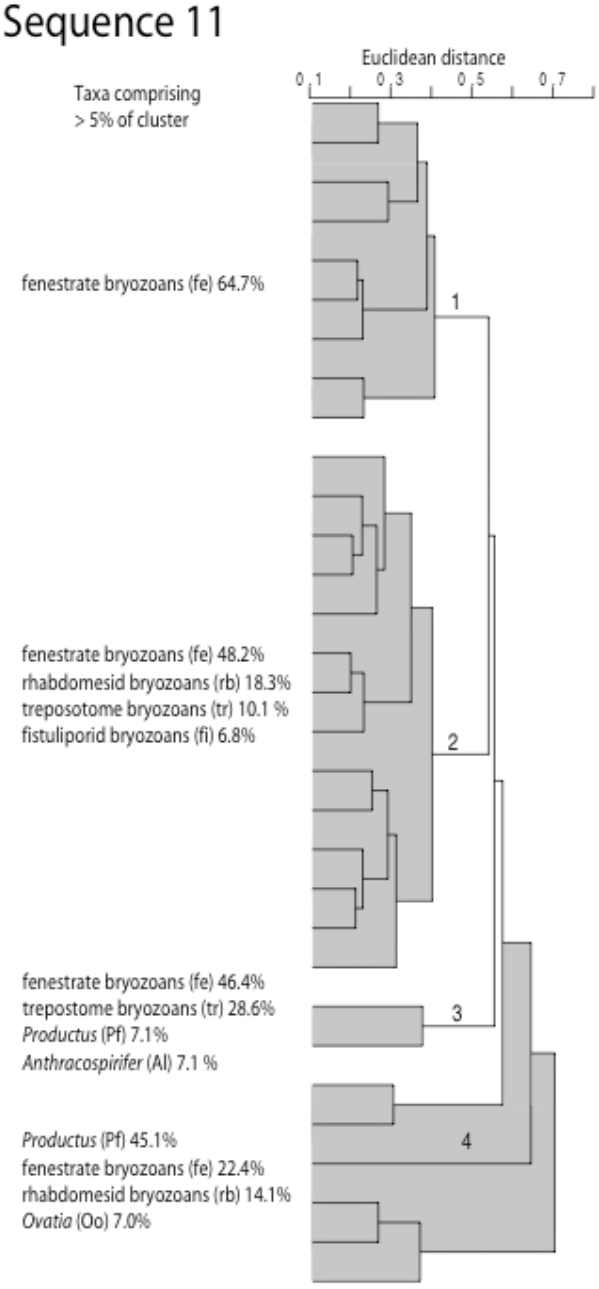

Taxa
sand rich
mud rich
inner ramp
outer ramp
DCA Axis 2
DCA Axis 1


Sequence 10
Euclidean distance
Taxa comprising
> 5% of cluster
fenestrate bryozoans (fe) 51.8%
rhabdomesid bryozoans (rb) 13.8%
trepostome bryozoans (tr) 5.2%
1
Reticulariina (Rs) 40.0%
fenestrate bryozoans (fe) 33.3%
Eumetria (Et) 13.3%
Orthotetes (Ok) 6.6%
Composita (Cp) 6.6%
2
fenestrate bryozoans (fe) 78.6%
fistuliporid bryozoans (fi) 5.0%
3
trepostome bryozoans (fe) 78.6%
Eumetria (Et) 21.1%
Cleiothyridina (Cs) 21.1%
Torynifer (Ts) 10.5%
Orthotetes (Ok) 5.3%
Reticulariina (Rs) 5.3%
Composita (Cp) 5.3%
4
Productus (Pf) 66.2%
trepostome bryozoans (tr) 22.3%
5
fenestrate bryozoans (fe) 96.1%
6


Biofacies
DCA Axis 2
DCA Axis 1


Depositional Environment
DCA Axis 2
DCA Axis 1


Taxa
inner ramp
middle ramp
DCA Axis 2
DCA Axis 1


Sequence 11
Euclidean distance
Taxa comprising
> 5% of cluster
fenestrate bryozoans (fe) 64.7%
fenestrate bryozoans (fe) 48.2%
rhabdomesid bryozoans (rb) 18.3%
treposotome bryozoans (tr) 10.1 %
fistuliporid bryozoans (fi) 6.8%
fenestrate bryozoans (fe) 46.4%
trepostome bryozoans (tr) 28.6%
Productus (Pf) 7.1%
Anthracospirifer (Al) 7.1 %
Productus (Pf) 45.1%
fenestrate bryozoans (fe) 22.4%
rhabdomesid bryozoans (rb) 14.1%
Ovatia (Oo) 7.0%

# Appendix B.

## Community Lists

The following supplementary lists were created for chapter 2. Each list shows the most abundant taxa in each depositional environment. Results are shown for all sampled depositional sequences.

SEQUENCE 1

| Backshoal | | Intershoal | | Skeletal Bank | |
|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| *Ovatia* | 45.6 | fenestrates | 48.3 | fenestrates | 31.4 |
| *Girtyella* | 27.3 | *Anthracospirifer* | 19.6 | *Lithostrotian* | 29.9 |
| *Anthracospirifer* | 7.4 | *Ovatia* | 6.5 | *Ovatia* | 17.5 |
| *Wilkingia* | 6.8 | *Productus* | 5.3 | *Productus* | 16.1 |
| *Martinia* | 5.2 | | | | |

SEQUENCE 5

| Backshoal | | Oolitic Shoal | |
|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance |
| *Anthracospirifer* | 83.7 | *Productus* | 31.0 |
| | | *Girtyella* | 27.6 |
| | | *Anthracospirifer* | 20.7 |
| | | fenestrates | 6.9 |
| | | *Ovatia* | 6.9 |

SEQUENCE 6

| Backshoal | | Intershoal | | Oolitic Shoal | | Skeletal Bank | |
|---|---|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| *Anthracospirifer* | 80.6 | *Productus* | 20.9 | *Productus* | 25.5 | fenestrates | 42.9 |
| | | fenestrates | 18.7 | *Ovatia* | 17.7 | *Productus* | 9.4 |
| | | *Martinia* | 15.8 | *Platyceras* | 13.5 | *Composita* | 8.1 |
| | | *Orthotetes* | 14.4 | *Martinia* | 11.3 | trepostomes | 6.9 |
| | | *Ovatia* | 9.4 | *Girtyella* | 7.1 | *Girtyella* | 5.7 |
| | | *Anthracospirifer* | 7.9 | *Anthracospiri* | 6.4 | | |
| | | | | rhabdomesids | 5.0 | | |

SEQUENCE 7

| Backshoal | | Skeletal Bank | | Foreshoal | |
|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| *Reticulariina* | 52.6 | fenestrates | 31.1 | *Productus* | 22.8 |
| fenestrates | 14.7 | *Reticulariina* | 15.8 | fenestrates | 16.7 |
| *Anthracospirifer* | 6.4 | trepostomes | 12.7 | trepostomes | 10.2 |
| trepostomes | 5.4 | rhabdomesids | 8.8 | *Ovatia* | 9.6 |
| fistuliporates | 5.3 | | | *Martinia* | 9.6 |
| | | | | *Dictyoclostus* | 9.1 |
| | | | | *Spirifer* | 8.1 |

SEQUENCE 9

| Skeletal Bank | | Foreshoal | |
|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance |
| fenestrates | 16.9 | *Productus* | 44.9 |
| *Martinia* | 9.1 | *Ovatia* | 26.6 |
| rhabdomesids | 8.8 | *Composita* | 5.8 |
| trepostomes | 8.8 | | |
| *Spirifer* | 7.8 | | |
| *Composita* | 7.8 | | |
| *Eumetria* | 5.2 | | |

SEQUENCE 10

| Tidal | | Backshoal | | Skeletal Shoal | |
|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| fenestrates | 58.5 | fenestrates | 75.4 | fenestrates | 72.7 |
| rhabdomesids | 9.9 | *Pentremites* | 7.8 | fistuliporates | 6.6 |
| trepostomes | 7.8 | | | rhabdomesids | 5.7 |
| *Reticulariina* | 6.3 | | | | |

SEQUENCE 10 (cont)

| Skeletal Bank | | Foreshoal | |
|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance |
| fenestrates | 59.5 | *Productus* | 59.7 |
| rhabdomesids | 11.4 | trepostomes | 19.3 |
| fistuliporates | 4.7 | fenestrates | 9.2 |

SEQUENCE 11

| Backshoal | | Skeletal Shoal | | Skeletal Bank | |
|---|---|---|---|---|---|
| Taxon | Percent Abundance | Taxon | Percent Abundance | Taxon | Percent Abundance |
| fenestrates | 63.6 | fenestrates | 34.5 | fenestrates | 46.1 |
| *Productus* | 7.0 | rhabdomesids | 17.5 | rhabdomesids | 17.2 |
| | | *Productus* | 10.1 | trepostomes | 12.3 |
| | | *Anthracospirifer* | 7.4 | fistuliporates | 8.3 |
| | | trepostomes | 7.1 | | |
| | | *Girtyella* | 6.8 | | |

# Appendix C.

## Sampling Localities

The following contains a description of the localities that were sampled in this study. Primary references that contain detailed stratigraphic sections and information on many other Chesterian outcrops in the study area are also included. Locality information was lumped together from outcrops that were less than 0.1 miles apart from each other.

Illinois Basin

1. Roadcut at junction of Indiana State Routes 62 and 462, ~ 2 mi. northwest of Corydon, Indiana – Ste. Genevieve Fm. (Dodd et al. 2001).

2. Roadcut at junction of Indiana State Route 62 and Walnut Valley Rd., ~ 2 mi. northwest of Corydon, Indiana – Ste. Genevieve Fm. (Dodd et al. 2001).

3. Roadcut on southbound side of Indiana State Route 135, just north of intersection with Squire Boone Cavern Rd. (across the street from Squire Boon Cavern Welcome Center), ~ 4 mi. south of Corydon, Indiana – Ste. Genevieve Fm. (Dodd et al. 2001).

4. Roadcut ~ 0.3 – 0.6 mi. south of intersection of Indiana State Route 62 and 135 near Corydon, Indiana – Ste. Genevieve Fm. (Hunter, 1993).

5. Roadcut ~ 4.0-4.4 mi. south of intersection of Indiana State Routes 62 and 135 near Corydon, Indiana – Ste. Genevieve Fm. (Hunter, 1993).

6. Roadcuts near mile marker 99 on Interstate 64 (Scout Mountain Roadcut), approximately 5.1 mi. west of Corydon, Indiana – St. Genvieve through Beaver Bend Fms. (Horowitz 1992; Dodd 2001; Smith and Read 2001).

7. Roadcut along Kentucky State Route 228 across from the Battletown Quarry, ~ 8.4 mi northwest of the town of Battletown – St. Genevieve through Beech Creek (Dever et al. 1977).

8. Roadcut on Indiana State Route 145, ~ 2.9 mi. south of the town of French Lick – Beaver Bend Fm. (Cody 1978).

9. Roadcut on Indiana State Route 145, ~ 3.3 mi. south of the town of French Lick – Beaver Bend Fm. (Cody 1978).

10. Roadcut on William Hatcher Parkway near mile marker 9.1, east of Bowling Green, Kentucky – Beaver Bend through Beech Creek Fms. (Smith and Read 2001).

11. Roadcut at junction of Interstate 64 and Indiana State Route 37 (mile marker 85.9), approximately 1 mi. north of Sulphur, Indiana. Outcrops are located on all 4 interstate ramps – Reelsville through Haney Fms. (Horowitz and Kelly 1987; Harris 1992; Horowitz 1992; Smith and Read 2001).

12. Roadcut on south side of Indiana State Route 62, just west of the Little Blue River,~ .75 miles northwest of town of Beechwood – Reelsville Fm. (Rexroad and Merrill 1996).

13. Roadcut on E. Temple Road (Old Indiana State Route 64), ~ 0.8 east of intersection with Indiana State Route 37 at town of English. Roadcut parallels railroad tracks – Reelsville Fm. (Rexroad and Merrill 1996).

14. Roadcut on US Route 150 ~ 2 mi west of town of Prospect, Indiana – Reelsville Fm. (Rexroad and Merrill 1996).

15. Roadcut on Interstate 64 in Indiana, ~ 1.0 mi. west of Scout Mountain cut – Sample and Reelsville Fms. (Horowitz 1992).

16. Roadcut at mile marker 98 on Interstate 64 in Indiana - Beech Creek Fm. (Harris 1992; Horowitz 1992).

17. Roadcut at mile marker 95.8 on Interstate 64 in Indiana - Beech Creek Fm. (Harris 1992; Horowitz 1992).

18. Roadcut at mile marker 94.4 on Interstate 64 in Indiana – Beech Creek Fm. (Harris 1992; Horowitz 1992).

19. Roadcut at mile marker 88.8 on Interstate 64 in Indiana – Beech Creek Fm. (Harris 1992; Horowitz 1992).

20. Roadcut on Indiana State Route 37, ~ 1.9 mi. south of the town of Grantsburg – Haney Fm.

21. Roadcuts at intersection of Indiana 37 N and country road 12 (at exit sign for town of Grantsburg) – Haney Fm.

22. Roadcuts on Wendell H. Ford Western Kentucky Parkway near mile marker 106.5 south of Leitchfield – Haney Fm. (Vincent 1975).

23. Roadcut located 0.2 mi south of the junction of Kentucky State Routes 75 and 105 near Rough River State Resort Park – Haney Fm. (Williamson et al. 1979).

24. Roadcut located 0.8 mi. south of the junction of Kentucky State Routes 75 and 105 near Rough River State Resort Park – Glen Dean Fm. (Williamson et al. 1979).

25. Roadcut on Indiana State Route145 across from Mulzer Brothers Quarry, just north of intersection with Indiana State Route 64 – Glen Dean Fm. (Horowitz 1956).

26. Roadcut located ~ 13.1 mi south of French Lick on Indiana State Route 145 N just across from Patoka Lake – Glen Dean Fm. (Williamson et al. 1979).

27. Natural exposure located off of Kentucky State Route 105 on an unnamed country road about 0.8 mi north of the town of Glen Dean. Type Glen Dean section (Horowitz 1956).

28. Roadcut near mile marker 15.5 on Wendell H. Ford Western Kentucky Parkway, just north of Princeton – Glen Dean Fm. (Smith and Read 2001).

29. Natural exposure located on country road 45 on hill behind boat mechanics shop, about 1 mi. to the noretheast of the town of Tobinsport, Indiana – Glen Dean (Horowitz 1956).

30. Roadcut located on the north side of Indiana State Route166, about 0.1 mi. south of junction with Indiana State Route 66 near town of Tobinsport – Glen Dean Fm. (Horowitz 1956).

Appalachian Basin

31. Roadcut on Kentucky State Route 519, just before junction with Kentucky State Route 1274, about 5 mi. south of the city of Morehead – Paoli through Haney Fms (Al-Tawil and Read 2003).

32. Roadcuts on Kentucky State Route 801, just west of junction with Kentucky State Route 1274 – Paoli through Glen Dean Fms. (Al-Tawil and Read 2003).

33. Roadcut near mile marker 159 on Interstate 64 in Kentucky – Beach Creek through Glen Dean Fms. (Read 1980; Al-Tawil and Read 2003).

34. Roadcut near mile marker 159.5 on Interstate 64 Kentucky – Reelsville through Glen Dean (Read 1980; Al-Tawil and Read 2003).

35. Roadcut near mile marker 158 on Interstate 64 in Kentucky - Beaver Bend through Haney Fms. (Read 1980; Al-Tawil and Read 2003).

36. Roadcuts along westbound and eastbound lanes of Interstate 64 behind weigh stations. Cuts are about 8.7 mi. west of intersection with Kentucky State Route 2 – Pre-Chesterian through Haney Fm. (Read 1980; Al-Tawil 2003).

37. Roadcut south of Mt. Vernon, Kentucky. Section begins at intersection of Kentucky State Routes 461 and 1326 and continues north along 461 – Pre-Chesterian through Glen Dean Fm. (Al-Tawil and Read 2003).

38. Roadcuts along east side of Kentucky Highway 1209 along Station Camp Creek, about 10 mi. south of junction with Kentucky Highway 89 – Pre-Chesterian through Glen Dean. (Al-Tawil and Read 2003)

39. Armstrong Hill roadcut on Kentucky State Route 2 at the intersection with Interstate 64 – Beaver Bend through Haney Fms. (Read 1980; Al-Tawil and Read 2003)

40. Roadcut on Kentucky State Route 182, located 0.9 mi. west from intersection US Route 60 – Reelsville through Haney Fms.

41. Roadcut on US Route 60 next to the AA Truck Repair Shop, about 0.1 mi from junction with Kentucky State Route 1025. Reelsville through Haney Fms.

42. Roadcut along Interstate 75 near mile marker 61, just south of Renfro Valley, Kentucky – Ste. Genevieve through Glen Dean Fms. (Al-Tawil and Read 2003).

43. Roadcut along northbound lane of Interstate 75, just south of the Jellico offramp, Jellico, Tennessee – Pre-Chesterian through Pennsylvanian. (Al-Tawil and Read 2003).

# Appendix D.

## Illinois Basin Data Matrix

The following abundance data matrix consists of 201 samples and 48 taxa. Sample names are listed at left and follow the format: Sequence-Environment-sample letter, where T is tidal, B is backshoal, I is intershoal, H is skeletal shoal, O is oolitic shoal, S is skeletal bank, and F is foreshoal. Samples are listed in order by sequence.

| | *Fenestellidae* | *Rhabdomisidae* | *Fistuliporidae* | *Trepostomata* | *Lingula* | *Orbiculoidea* | *Schellwienella* | *Schuchertella* | *Orthotetes* | *Chonetes* | *Dictyoclostus* | *Productus* | *Ovatia* | *Echinoconchus* | *Buxtonia* | *Rhyncopora* | *Dielasma* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S1-I-a | 31 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 8 | 5 | 0 | 0 | 0 | 0 |
| S1-I-b | 30 | 3 | 3 | 7 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| S1-I-c | 19 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 3 | 8 | 3 | 0 | 0 | 0 | 0 |
| S1-I-d | 26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 4 | 1 | 0 |
| S1-I-e | 31 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 8 | 1 | 0 | 0 | 0 |
| S1-I-f | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 2 | 0 | 0 | 0 | 0 |
| S1-I-g | 89 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 2 | 7 | 11 | 0 | 0 | 0 | 0 |
| S1-I-h | 49 | 5 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 2 | 0 | 3 | 0 | 0 |
| S1-I-I | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 12 | 0 | 1 | 0 | 0 |
| S1-I-j | 34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 7 | 0 | 0 | 1 | 0 |
| S1-I-k | 56 | 3 | 8 | 0 | 0 | 3 | 0 | 0 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S1-I-l | 4 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S1-I-m | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S1-I-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S1-I-p | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-q | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-n | 22 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S1-B-a | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 21 | 0 | 0 | 0 | 0 |
| S1-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 0 | 0 | 0 | 0 |
| S1-B-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 30 | 0 | 0 | 0 | 2 |
| S1-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 47 | 0 | 0 | 0 | 0 |
| S1-B-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 38 | 0 | 0 | 0 | 0 |
| S1-S-a | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 17 | 0 | 0 | 0 | 0 |
| S1-S-b | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 4 | 0 | 0 | 0 | 0 |
| S1-S-c | 16 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 7 | 3 | 0 | 0 | 0 | 0 |
| S5-B-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-c | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S5-B-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-O-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-O-b | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| S5-O-c | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 |
| S5-O-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| S6-S-a | 58 | 0 | 0 | 9 | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-b | 49 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S6-S-c | 67 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-d | 33 | 0 | 0 | 9 | 0 | 0 | 0 | 1 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Fenestellidae* | *Rhabdomisidae* | *Fistuliporidae* | *Trepostomata* | *Lingula* | *Orbiculoidea* | *Schellwienella* | *Schuchertella* | *Orthotetes* | *Chonetes* | *Dictyoclostus* | *Productus* | *Ovatia* | *Echinoconchus* | *Buxtonia* | *Rhynchopora* | *Dielasma* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S6-S-e | 44 | 5 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-f | 27 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 27 | 1 | 0 | 0 | 0 | 0 |
| S6-S-g | 8 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| S6-S-h | 21 | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S6-S-I | 4 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 3 | 0 | 1 | 32 | 1 | 0 | 0 | 0 | 4 |
| S6-S-j | 16 | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 31 | 0 | 0 | 0 | 0 | 0 |
| S6-S-k | 29 | 1 | 0 | 8 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-l | 19 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 2 | 1 | 0 | 0 | 0 | 0 |
| S6-S-m | 50 | 2 | 0 | 20 | 0 | 0 | 0 | 2 | 4 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| S6-S-n | 32 | 11 | 0 | 4 | 0 | 0 | 0 | 1 | 2 | 0 | 5 | 6 | 0 | 0 | 0 | 0 | 0 |
| S6-S-o | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
| S6-S-p | 6 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 11 | 0 | 0 | 0 | 0 | 0 |
| S6-S-q | 73 | 13 | 0 | 9 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 |
| S6-O-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 4 | 0 | 0 | 0 | 0 |
| S6-O-b | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 19 | 11 | 0 | 0 | 0 | 0 |
| S6-O-c | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 |
| S6-I-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 0 |
| S6-I-b | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 9 | 1 | 0 | 0 | 0 | 0 |
| S6-I-c | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-d | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 10 | 0 | 0 | 0 | 0 |
| S6-I-e | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 |
| S6-I-f | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 10 | 3 | 0 | 0 | 0 | 0 |
| S6-I-g | 9 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 5 | 1 | 0 | 0 | 0 | 0 |
| S6-I-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 0 |
| S6-B-a | 3 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-B-b | 0 | 1 | 0 | 5 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-B-c | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| S7-S-a | 39 | 9 | 0 | 6 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S7-S-b | 39 | 6 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| S7-S-c | 34 | 11 | 0 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-d | 41 | 5 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S7-S-e | 28 | 11 | 6 | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| S7-S-f | 54 | 20 | 20 | 32 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 5 | 0 | 0 | 0 | 0 |
| S7-S-g | 56 | 32 | 15 | 37 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 |
| S7-S-h | 23 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-I | 57 | 7 | 17 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S7-S-j | 8 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| S7-S-k | 4 | 11 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 14 | 3 | 2 | 0 | 0 | 0 |
| S7-S-l | 3 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 6 | 1 | 0 | 0 | 0 | 0 |
| S7-S-m | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S7-S-n | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 7 | 2 | 0 | 0 | 0 | 0 |
| S7-S-o | 9 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |

| | *Fenestellidae* | *Rhabdomisidae* | *Fistuliporidae* | *Trepostomata* | *Lingula* | *Orbiculoidea* | *Schellwienella* | *Schuchertella* | *Orthotetes* | *Chonetes* | *Dictyoclostus* | *Productus* | *Ovatia* | *Echinoconchus* | *Buxtonia* | *Rhyncopora* | *Dielasma* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S10-S-I | 112 | 13 | 5 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 |
| S10-S-j | 63 | 5 | 6 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 6 | 2 | 0 | 0 | 2 |
| S10-B-a | 16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| S10-B-b | 32 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-B-c | 64 | 4 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S10-B-d | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S10-T-a | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-b | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-c | 28 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-d | 39 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-e | 85 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-f | 28 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-g | 30 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-h | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-I | 17 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-j | 6 | 2 | 3 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-k | 2 | 10 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-l | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-m | 7 | 5 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-n | 18 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-o | 15 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-p | 11 | 5 | 5 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-q | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-r | 6 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 |
| S10-T-s | 45 | 24 | 4 | 15 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-t | 155 | 10 | 2 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| S10-T-u | 6 | 14 | 4 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-v | 8 | 6 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| S10-H-a | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-b | 18 | 16 | 1 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-c | 147 | 0 | 21 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-d | 73 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S10-F-a | 20 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 |
| S10-F-b | 2 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 0 |
| S10-F-c | 0 | 2 | 0 | 5 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 77 | 1 | 0 | 0 | 0 | 0 |
| S10-F-d | 0 | 0 | 0 | 39 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 46 | 0 | 0 | 0 | 0 | 0 |
| S10-O-a | 1 | 6 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S10-O-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-H-a | 3 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S11-H-b | 15 | 10 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 |
| S11-H-c | 15 | 32 | 1 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S11-H-d | 55 | 9 | 1 | 6 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

| | *Fenestellidae* | *Rhabdomisididae* | *Fistuliporidae* | *Trepostomata* | *Lingula* | *Orbiculoidea* | *Schellwienella* | *Schuchertella* | *Orthotetes* | *Chonetes* | *Dictyoclostus* | *Productus* | *Ovatia* | *Echinoconchus* | *Buxtonia* | *Rhyncopora* | *Dielasma* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S11-H-e | 9 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| S11-H-f | 12 | 10 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S11-H-g | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 5 | 0 | 0 | 0 | 0 |
| S11-H-h | 13 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-B-a | 13 | 5 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| S11-B-b | 29 | 8 | 4 | 9 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| S11-B-c | 395 | 0 | 6 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 2 | 0 | 0 | 0 | 1 |
| S11-B-d | 9 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 31 | 4 | 0 | 0 | 0 | 0 |
| S11-B-e | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 27 | 3 | 0 | 0 | 0 | 1 |
| S11-B-f | 107 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 27 |
| S11-B-g | 84 | 11 | 0 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 13 | 0 | 0 | 0 | 0 | 19 |
| S11-B-h | 130 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 |
| S11-S-a | 4 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S11-S-b | 45 | 2 | 26 | 17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-c | 3 | 0 | 30 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S11-S-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S11-S-f | 116 | 18 | 6 | 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| S11-S-g | 14 | 1 | 7 | 7 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 12 | 1 | 0 | 0 | 0 | 0 |
| S11-S-h | 17 | 11 | 8 | 58 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 2 |
| S11-S-I | 8 | 13 | 7 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| S11-S-j | 48 | 31 | 28 | 25 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S11-S-k | 19 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-l | 53 | 61 | 4 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S11-S-m | 41 | 13 | 1 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S11-S-n | 72 | 56 | 9 | 12 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S11-S-o | 145 | 9 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-p | 60 | 31 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Girtyella* | *Punctospirifer* | *Reticulariina* | *Spirifer* | *Anthracospirifer* | *Torynifer* | *Martinia* | *Eumetria* | *Athyris* | *Cleiothyridina* | *Composita* | *Pentremites* | *Aviculopecten* | *Edmondia* | *Nuculopsis* | *Wilkingia* | *Euomphalus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S6-S-e | 3 | 6 | 5 | 2 | 2 | 0 | 0 | 0 | 0 | 3 | 3 | 4 | 0 | 0 | 0 | 0 | 0 |
| S6-S-f | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-g | 2 | 5 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-h | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-I | 2 | 1 | 1 | 0 | 8 | 1 | 0 | 2 | 0 | 12 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-j | 6 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-k | 2 | 2 | 5 | 0 | 1 | 0 | 0 | 2 | 0 | 4 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-l | 7 | 3 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 3 | 8 | 1 | 0 | 0 | 0 | 0 | 0 |
| S6-S-m | 9 | 3 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 17 | 2 | 0 | 0 | 0 | 0 | 0 |
| S6-S-n | 3 | 2 | 5 | 0 | 1 | 0 | 1 | 0 | 0 | 3 | 11 | 2 | 0 | 0 | 0 | 0 | 0 |
| S6-S-o | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S6-S-p | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-q | 13 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 5 | 9 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-O-a | 4 | 0 | 0 | 0 | 2 | 0 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-O-b | 4 | 0 | 0 | 0 | 1 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-O-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-a | 1 | 0 | 0 | 0 | 1 | 0 | 12 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-b | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-d | 2 | 0 | 0 | 0 | 4 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-e | 1 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-f | 2 | 0 | 0 | 0 | 3 | 0 | 4 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-g | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-h | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-B-a | 0 | 0 | 0 | 0 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-B-b | 0 | 0 | 0 | 0 | 37 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-B-c | 0 | 0 | 0 | 0 | 75 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-a | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S7-S-b | 2 | 3 | 32 | 0 | 8 | 0 | 0 | 8 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| S7-S-c | 1 | 3 | 16 | 2 | 1 | 0 | 0 | 3 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| S7-S-d | 9 | 0 | 11 | 0 | 7 | 0 | 0 | 7 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S7-S-e | 13 | 0 | 20 | 0 | 4 | 0 | 0 | 5 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S7-S-f | 6 | 1 | 40 | 0 | 8 | 0 | 0 | 1 | 0 | 1 | 0 | 11 | 0 | 0 | 0 | 0 | 0 |
| S7-S-g | 0 | 0 | 42 | 0 | 5 | 0 | 0 | 6 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| S7-S-h | 8 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-I | 11 | 0 | 18 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-j | 1 | 0 | 19 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 |
| S7-S-k | 0 | 0 | 0 | 2 | 2 | 0 | 35 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-l | 0 | 0 | 0 | 1 | 0 | 0 | 17 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-m | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-n | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Girtyella* | *Punctospirifer* | *Reticulariina* | *Spirifer* | *Anthracospirifer* | *Torynifer* | *Martinia* | *Eumetria* | *Athyris* | *Cleiothyridina* | *Composita* | *Pentremites* | *Aviculopecten* | *Edmondia* | *Nuculopsis* | *Wilkingia* | *Euomphalus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S7-B-a | 0 | 0 | 63 | 0 | 6 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-B-b | 3 | 0 | 192 | 0 | 24 | 0 | 0 | 10 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-B-c | 1 | 1 | 59 | 0 | 8 | 0 | 0 | 1 | 0 | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 0 |
| S7-B-d | 0 | 3 | 5 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-B-e | 1 | 4 | 43 | 0 | 2 | 0 | 0 | 5 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |
| S7-B-f | 0 | 0 | 7 | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-a | 1 | 0 | 0 | 1 | 10 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-b | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-c | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| S7-F-d | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| S7-F-e | 0 | 0 | 0 | 11 | 2 | 0 | 44 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-f | 0 | 0 | 1 | 17 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-g | 0 | 2 | 3 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-h | 0 | 0 | 2 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-a | 0 | 1 | 2 | 14 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 |
| S9-S-b | 0 | 0 | 5 | 5 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-c | 2 | 0 | 1 | 13 | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-d | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| S9-S-e | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| S9-S-f | 0 | 1 | 1 | 8 | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-g | 0 | 0 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-h | 2 | 2 | 4 | 4 | 0 | 0 | 1 | 1 | 0 | 0 | 9 | 1 | 0 | 0 | 0 | 0 | 0 |
| S9-S-I | 0 | 0 | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| S9-S-j | 3 | 0 | 5 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| S9-S-k | 15 | 2 | 6 | 0 | 1 | 0 | 2 | 0 | 7 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S9-F-a | 0 | 16 | 7 | 5 | 2 | 1 | 21 | 20 | 0 | 8 | 14 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-b | 0 | 6 | 1 | 8 | 6 | 0 | 6 | 12 | 0 | 4 | 15 | 0 | 0 | 0 | 1 | 0 | 0 |
| S9-F-c | 0 | 8 | 2 | 3 | 1 | 0 | 42 | 10 | 0 | 6 | 5 | 0 | 0 | 0 | 2 | 5 | 1 |
| S9-F-d | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-e | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-f | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-g | 13 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-h | 0 | 0 | 4 | 6 | 0 | 0 | 0 | 1 | 0 | 2 | 9 | 1 | 0 | 0 | 0 | 0 | 0 |
| S9-F-I | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-a | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S10-S-b | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-c | 1 | 1 | 2 | 0 | 6 | 0 | 0 | 1 | 0 | 2 | 10 | 11 | 0 | 0 | 0 | 0 | 0 |
| S10-S-d | 0 | 5 | 5 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 4 | 11 | 0 | 0 | 0 | 0 | 0 |
| S10-S-e | 0 | 1 | 11 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 7 | 2 | 0 | 0 | 0 | 0 | 0 |
| S10-S-f | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 1 | 0 | 5 | 5 | 5 | 0 | 0 | 0 | 0 | 0 |
| S10-S-g | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 6 | 2 | 5 | 0 | 0 | 0 | 0 | 0 |
| S10-S-h | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Girtyella* | *Punctospirifer* | *Reticulariina* | *Spirifer* | *Anthracospirifer* | *Torynifer* | *Martinia* | *Eumetria* | *Athyris* | *Cleiothyridina* | *Composita* | *Pentremites* | *Aviculopecten* | *Edmondia* | *Nucuclopsis* | *Wilkingia* | *Euomphalus* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S10-S-I | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 5 | 6 | 0 | 0 | 0 | 0 | 0 |
| S10-S-j | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 6 | 0 | 3 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| S10-B-a | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S10-B-b | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-B-c | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 9 | 0 | 0 | 0 | 0 | 0 |
| S10-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 0 | 0 | 0 | 0 | 0 |
| S10-T-a | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-d | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-e | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-g | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S10-T-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 |
| S10-T-j | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-k | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-l | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-m | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-n | 0 | 1 | 5 | 0 | 0 | 0 | 0 | 2 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-o | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-p | 0 | 1 | 10 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-q | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-r | 0 | 0 | 7 | 2 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-s | 1 | 1 | 3 | 10 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-t | 0 | 1 | 2 | 21 | 0 | 1 | 2 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-u | 0 | 1 | 4 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-v | 0 | 2 | 3 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 |
| S10-H-b | 0 | 2 | 6 | 0 | 0 | 0 | 0 | 7 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-c | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-d | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-a | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-b | 0 | 1 | 0 | 3 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-c | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-O-a | 0 | 0 | 0 | 0 | 2 | 0 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-O-b | 0 | 0 | 1 | 0 | 1 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-H-a | 4 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-H-b | 15 | 0 | 1 | 4 | 4 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 0 | 0 |
| S11-H-c | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S11-H-d | 0 | 0 | 2 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Euphemites* | *Globozyga* | *Naticopsis* | *Paleozygopleura* | *Platyceras* | *Strophostylus* | *Trepospira* | *Orthoceras* | *Triptoceroides* | *Triplophyllites* | *Columnaria* | *Lithostrotian* | *Paladin* | *Conulariid* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S1-I-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-k | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-l | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-m | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-p | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-q | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-I-n | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-B-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S1-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-B-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-B-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-S-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S1-S-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 16 | 0 | 0 |
| S1-S-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 0 | 0 |
| S5-B-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S5-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S5-B-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-B-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S5-B-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S5-O-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-O-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S5-O-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S5-O-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S6-S-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Euphemites* | *Globozyga* | *Naticopsis* | *Paleozygopleura* | *Platyceras* | *Strophostylus* | *Trepospira* | *Orthoceras* | *Triptoceroides* | *Triplophyllites* | *Columnaria* | *Lithostrotian* | *Paladin* | *Conulariid* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S6-S-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S6-S-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| S6-S-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| S6-S-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-k | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S6-S-l | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S6-S-m | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-n | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-p | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-S-q | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-O-a | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-O-b | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S6-O-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S6-I-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S6-I-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-d | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-I-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-B-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S6-B-b | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S6-B-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 |
| S7-S-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S7-S-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 11 | 0 | 0 | 0 | 0 |
| S7-S-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| S7-S-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| S7-S-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 0 |
| S7-S-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| S7-S-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S7-S-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| S7-S-k | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-l | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-m | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S7-S-n | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-S-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

| | *Euphemites* | *Globozyga* | *Naticopsis* | *Paleozygopleura* | *Platyceras* | *Strophostylus* | *Trepospira* | *Orthoceras* | *Triptoceroides* | *Triplophyllites* | *Columnaria* | *Lithostrotian* | *Paladin* | *Conulariid* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S7-B-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S7-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| S7-B-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| S7-B-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 |
| S7-B-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S7-F-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S7-F-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| S7-F-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S7-F-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S9-S-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 |
| S9-S-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 |
| S9-S-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| S9-S-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-S-k | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-a | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-c | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S9-F-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S9-F-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S10-S-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| S10-S-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S10-S-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| S10-S-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Euphemites* | *Globozyga* | *Naticopsis* | *Paleozygopleura* | *Platyceras* | *Strophostylus* | *Trepospira* | *Orthoceras* | *Triptoceroides* | *Triplophyllites* | *Columnaria* | *Lithostrotian* | *Paladin* | *Conulariid* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S10-S-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S10-S-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S10-B-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-B-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| S10-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| S10-T-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-k | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-l | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-m | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-n | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-p | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-q | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-r | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-s | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-t | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-u | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-v | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-H-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S10-H-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-O-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-O-b | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-H-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S11-H-b | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 |
| S11-H-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S11-H-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Euphemites* | *Globozyga* | *Naticopsis* | *Paleozygopleura* | *Platyceras* | *Strophostylus* | *Trepospira* | *Orthoceras* | *Triptoceroides* | *Triplophyllites* | *Columnaria* | *Lithostrotian* | *Paladin* | *Conulariid* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S11-H-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-H-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-H-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-H-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| S11-B-a | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| S11-B-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-B-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-B-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-B-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S11-B-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-B-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-h | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-I | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-k | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-l | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-m | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-n | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-p | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

# Appendix E.

## Appalachian Basin Data Matrix

The following abundance data matrix is comprised of 74 samples and 28 taxa from the Haney and Glen Dean Formations in the Appalachian Basin. Samples are listed at left and follow the format: Sequence-Environment-sample letter, where T is tidal, B is backshoal, S is skeletal bank, SI is silty skeletal bank, and F is foreshoal.

| | *Fenestellidae* | *Rhabdomesidae* | *Fistuliporidae* | *Trepostomata* | *Orbiculoidea* | *Schellwienella* | *Orthotetes* | *Dictyoclostus* | *Productus* | *Ovatia* | *Echinoconchus* | *Dielasma* | *Girtyella* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S10-F-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-aa | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-b | 3 | 0 | 0 | 4 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-bb | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-c | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-cc | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-d | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 9 | 0 | 0 | 0 | 0 |
| S10-F-dd | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 |
| S10-F-f | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 |
| S10-F-g | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S10-F-h | 3 | 6 | 0 | 0 | 0 | 0 | 5 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-F-I | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 58 | 0 | 0 | 0 | 0 |
| S10-F-j | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 34 | 0 | 0 | 0 | 0 |
| S10-F-k | 2 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 36 | 0 | 0 | 0 | 0 |
| S10-F-l | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 0 |
| S10-F-m | 9 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 |
| S10-F-n | 6 | 0 | 0 | 0 | 1 | 0 | 13 | 0 | 9 | 0 | 0 | 0 | 0 |
| S10-F-o | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 27 | 0 | 0 | 0 | 0 |
| S10-F-p | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-F-q | 33 | 2 | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-F-r | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-s | 1 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S10-F-t | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-F-u | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S10-F-v | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| S10-F-w | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| S10-F-x | 1 | 3 | 0 | 2 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | 0 |
| S10-F-y | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S10-F-z | 4 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 7 | 0 | 0 | 0 | 0 |
| S10-S-a | 7 | 7 | 0 | 1 | 0 | 0 | 6 | 3 | 2 | 0 | 0 | 0 | 0 |
| S10-S-b | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 0 | 0 | 0 | 0 |
| S10-S-c | 2 | 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-d | 11 | 7 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-e | 2 | 1 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-f | 14 | 12 | 0 | 19 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| S10-S-g | 7 | 10 | 1 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| S10-S-h | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 40 | 0 | 0 | 0 | 0 |
| S10-S-I | 6 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 15 | 0 | 0 | 0 | 0 |
| S10-S-j | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 32 | 0 | 0 | 0 | 0 |
| S10-S-k | 34 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-l | 6 | 5 | 0 | 10 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |

| | *Fenestelllidae* | *Rhabdomisidae* | *Fistuliporidae* | *Trepostomata* | *Orbiculoidea* | *Schellwienella* | *Orthotetes* | *Dictyoclostus* | *Productus* | *Ovatia* | *Echinoconchus* | *Dielasma* | *Girtyella* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S10-S-m | 34 | 11 | 0 | 16 | 1 | 1 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| S10-S-n | 4 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 4 | 1 | 0 | 0 | 0 |
| S10-T-a | 39 | 5 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-b | 23 | 5 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-T-c | 6 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 |
| S10-T-d | 14 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 |
| S11-F-a | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-b | 1 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S11-F-c | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S11-F-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| S11-F-e | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| S11-F-f | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-g | 0 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 1 | 0 | 0 | 0 |
| S11-F-h | 1 | 2 | 3 | 2 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-I | 7 | 10 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-j | 3 | 4 | 0 | 0 | 0 | 0 | 10 | 0 | 1 | 0 | 0 | 0 | 0 |
| S11-F-k | 0 | 1 | 0 | 10 | 0 | 0 | 15 | 0 | 1 | 0 | 0 | 0 | 0 |
| S11-F-l | 18 | 0 | 0 | 47 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-SI-a | 76 | 15 | 6 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| S11-SI-b | 154 | 53 | 4 | 10 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| S11-SI-c | 55 | 10 | 18 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| S11-SI-d | 375 | 31 | 30 | 20 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 1 |
| S11-SI-e | 7 | 9 | 1 | 8 | 0 | 0 | 3 | 0 | 1 | 1 | 0 | 0 | 0 |
| S11-SI-f | 59 | 26 | 10 | 3 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-SI-g | 113 | 20 | 0 | 9 | 0 | 0 | 6 | 0 | 2 | 0 | 0 | 1 | 0 |
| S10-B-a | 40 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 1 |
| S10-B-b | 40 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-a | 15 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 1 | 0 |
| S11-S-b | 56 | 4 | 0 | 9 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| S11-S-c | 38 | 1 | 0 | 10 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| S11-S-d | 15 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 |
| S11-S-e | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 0 | 0 |

| | *Punctospirifer* | *Reticulariina* | *Anthracospirifer* | *Spirifer* | *Toryinfer* | *Martinia* | *Eumetria* | *Athyris* | *Cleiothyridina* | *Composita* | *Pentremites* | *Limipecten* | *Platyceras* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S10-F-a | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-aa | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-b | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 0 | 0 | 0 |
| S10-F-bb | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| S10-F-c | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| S10-F-cc | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-d | 0 | 0 | 11 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-dd | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-e | 0 | 0 | 8 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-f | 0 | 0 | 16 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 |
| S10-F-g | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| S10-F-h | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| S10-F-I | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-j | 0 | 0 | 9 | 0 | 0 | 2 | 1 | 0 | 0 | 4 | 0 | 0 | 0 |
| S10-F-k | 0 | 0 | 17 | 0 | 0 | 1 | 2 | 0 | 0 | 7 | 0 | 0 | 0 |
| S10-F-l | 0 | 0 | 7 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-m | 0 | 1 | 25 | 0 | 0 | 6 | 1 | 0 | 2 | 0 | 0 | 5 | 0 |
| S10-F-n | 0 | 0 | 4 | 0 | 0 | 22 | 0 | 0 | 1 | 0 | 0 | 4 | 0 |
| S10-F-o | 0 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 |
| S10-F-p | 0 | 0 | 1 | 0 | 0 | 16 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| S10-F-q | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-r | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| S10-F-s | 0 | 2 | 27 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-t | 0 | 1 | 73 | 0 | 0 | 5 | 3 | 0 | 1 | 1 | 0 | 0 | 0 |
| S10-F-u | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-F-v | 0 | 0 | 9 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 1 | 0 | 0 |
| S10-F-w | 0 | 0 | 25 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| S10-F-x | 0 | 0 | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 |
| S10-F-y | 0 | 0 | 5 | 0 | 0 | 3 | 2 | 0 | 2 | 2 | 0 | 0 | 0 |
| S10-F-z | 0 | 0 | 7 | 0 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-a | 0 | 0 | 0 | 0 | 0 | 272 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| S10-S-b | 0 | 0 | 1 | 0 | 0 | 76 | 1 | 0 | 0 | 3 | 0 | 0 | 0 |
| S10-S-c | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-d | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-e | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 5 | 0 | 0 | 0 |
| S10-S-f | 0 | 0 | 26 | 0 | 0 | 1 | 5 | 1 | 0 | 0 | 0 | 0 | 0 |
| S10-S-g | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-h | 0 | 0 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| S10-S-I | 0 | 0 | 41 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 0 | 0 | 0 |
| S10-S-j | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-k | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-S-l | 0 | 0 | 5 | 0 | 0 | 0 | 3 | 0 | 1 | 1 | 0 | 0 | 0 |

| | *Punctospirifer* | *Reticulariina* | *Anthracospirifer* | *Spirifer* | *Torynifer* | *Martinia* | *Eumetria* | *Athyris* | *Cleiothyridina* | *Composita* | *Pentremites* | *Limipecten* | *Platyceras* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| S10-S-m | 1 | 0 | 44 | 0 | 0 | 6 | 7 | 0 | 0 | 10 | 0 | 0 | 0 |
| S10-S-n | 0 | 0 | 6 | 0 | 0 | 2 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-a | 1 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-b | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| S10-T-c | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-T-d | 0 | 12 | 6 | 0 | 0 | 0 | 7 | 0 | 18 | 0 | 0 | 0 | 0 |
| S11-F-a | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| S11-F-b | 0 | 2 | 27 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-c | 0 | 1 | 73 | 0 | 0 | 5 | 3 | 0 | 1 | 1 | 0 | 0 | 0 |
| S11-F-d | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-e | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-f | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| S11-F-g | 0 | 0 | 6 | 0 | 0 | 0 | 1 | 0 | 1 | 5 | 0 | 0 | 0 |
| S11-F-h | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 |
| S11-F-I | 0 | 1 | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-F-j | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| S11-F-k | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 0 |
| S11-F-l | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 |
| S11-SI-a | 0 | 0 | 2 | 2 | 0 | 0 | 3 | 0 | 2 | 1 | 1 | 0 | 1 |
| S11-SI-b | 0 | 3 | 2 | 2 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 | 0 |
| S11-SI-c | 0 | 4 | 1 | 4 | 0 | 0 | 3 | 0 | 5 | 0 | 2 | 0 | 6 |
| S11-SI-d | 2 | 3 | 1 | 1 | 0 | 0 | 4 | 0 | 3 | 2 | 3 | 0 | 0 |
| S11-SI-e | 0 | 2 | 4 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| S11-SI-f | 0 | 2 | 0 | 7 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-SI-g | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-B-a | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S10-B-b | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-a | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-b | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-c | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-d | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| S11-S-e | 0 | 0 | 0 | 0 | 0 | 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | Triplophyllites | Paladin |
|---|---|---|
| S10-F-a | 0 | 0 |
| S10-F-aa | 0 | 0 |
| S10-F-b | 0 | 1 |
| S10-F-bb | 0 | 0 |
| S10-F-c | 0 | 0 |
| S10-F-cc | 0 | 0 |
| S10-F-d | 0 | 0 |
| S10-F-dd | 0 | 0 |
| S10-F-e | 0 | 0 |
| S10-F-f | 0 | 0 |
| S10-F-g | 0 | 0 |
| S10-F-h | 0 | 0 |
| S10-F-I | 0 | 0 |
| S10-F-j | 0 | 0 |
| S10-F-k | 0 | 0 |
| S10-F-l | 0 | 0 |
| S10-F-m | 0 | 0 |
| S10-F-n | 0 | 0 |
| S10-F-o | 0 | 0 |
| S10-F-p | 1 | 0 |
| S10-F-q | 0 | 0 |
| S10-F-r | 0 | 0 |
| S10-F-s | 0 | 0 |
| S10-F-t | 0 | 0 |
| S10-F-u | 1 | 0 |
| S10-F-v | 0 | 0 |
| S10-F-w | 0 | 0 |
| S10-F-x | 0 | 0 |
| S10-F-y | 0 | 0 |
| S10-F-z | 0 | 0 |
| S10-S-a | 0 | 0 |
| S10-S-b | 0 | 0 |
| S10-S-c | 0 | 0 |
| S10-S-d | 0 | 0 |
| S10-S-e | 0 | 0 |
| S10-S-f | 0 | 0 |
| S10-S-g | 0 | 0 |
| S10-S-h | 0 | 0 |
| S10-S-I | 0 | 0 |
| S10-S-j | 0 | 0 |
| S10-S-k | 0 | 0 |
| S10-S-l | 0 | 0 |

| | Triplophyllites | Paladin |
|---|---|---|
| S10-S-m | 0 | 0 |
| S10-S-n | 0 | 1 |
| S10-T-a | 2 | 0 |
| S10-T-b | 0 | 0 |
| S10-T-c | 0 | 0 |
| S10-T-d | 0 | 0 |
| S11-F-a | 0 | 0 |
| S11-F-b | 0 | 0 |
| S11-F-c | 0 | 0 |
| S11-F-d | 0 | 0 |
| S11-F-e | 0 | 0 |
| S11-F-f | 0 | 0 |
| S11-F-g | 0 | 0 |
| S11-F-h | 1 | 0 |
| S11-F-I | 1 | 0 |
| S11-F-j | 1 | 0 |
| S11-F-k | 2 | 0 |
| S11-F-l | 2 | 0 |
| S11-SI-a | 0 | 1 |
| S11-SI-b | 0 | 1 |
| S11-SI-c | 0 | 2 |
| S11-SI-d | 0 | 0 |
| S11-SI-e | 0 | 0 |
| S11-SI-f | 0 | 0 |
| S11-SI-g | 0 | 0 |
| S10-B-a | 0 | 0 |
| S10-B-b | 1 | 0 |
| S11-S-a | 0 | 0 |
| S11-S-b | 0 | 0 |
| S11-S-c | 0 | 0 |
| S11-S-d | 0 | 0 |
| S11-S-e | 4 | 0 |

# Vita

**James Rocco Bonelli Jr.**

## Education

Summer 2008 - Ph.D., Department of Geosciences, The Pennsylvania State University
May 2003 - M.S., Geology Department, University of Cincinnati
June 2001 – B.A., Geology Department, Hofstra University

## Research Interests

Stratigraphic paleobiology, stratigraphy, sedimentology.

## Refereed Publications

**Bonelli, J. R. Jr.**, Patzkowsky, M. E. Accepted. How are global patterns of faunal turnover expressed at regional scales? Evidence from the Upper Mississippian (Chesterian Series), Illinois Basin, USA. PALAIOS 2008.

Brett, C. E., Hendy, A., Bartholomew, A., **Bonelli, J. R. Jr**., and McLaughlin, P. 2007. Response of shallow marine biotas to sea-level fluctuations: A review of faunal replacement and the process of habitat tracking. PALAIOS v. 22, pp. 230-246.

**Bonelli, J. R. Jr**., Brett, C. E., Miller, A. I., and Bennington, J B. 2006. Testing for faunal stability across a regional biotic transition: Stasis and variation among coral biofacies in the middle Devonian of the Appalachian Basin. *Paleobiology* v. 32 (1), pp. 20-37.

## Academic Honors and Awards

2007 - Chevron Scholarship
2006 - Scholten-Williams-Wright Scholarship Award, Department of Geosciences (PSU)
2005 - Geological Society of America Research Grant Award
2005 - Theodore Roosevelt Memorial Grant Award, American Museum of Natural History
2005 - Stephen J. Gould Grant Award, The Paleontological Society
2003 - Graduate Student Teaching Award, Department of Geology (UC)
2001 - Rawlinson Award, Department of Geology (UC)
2000 - Angelo Tagliacozza Memorial Geological Scholarship Award

## Professional Memberships

1). Paleontological Society
2). The Geological Society of America